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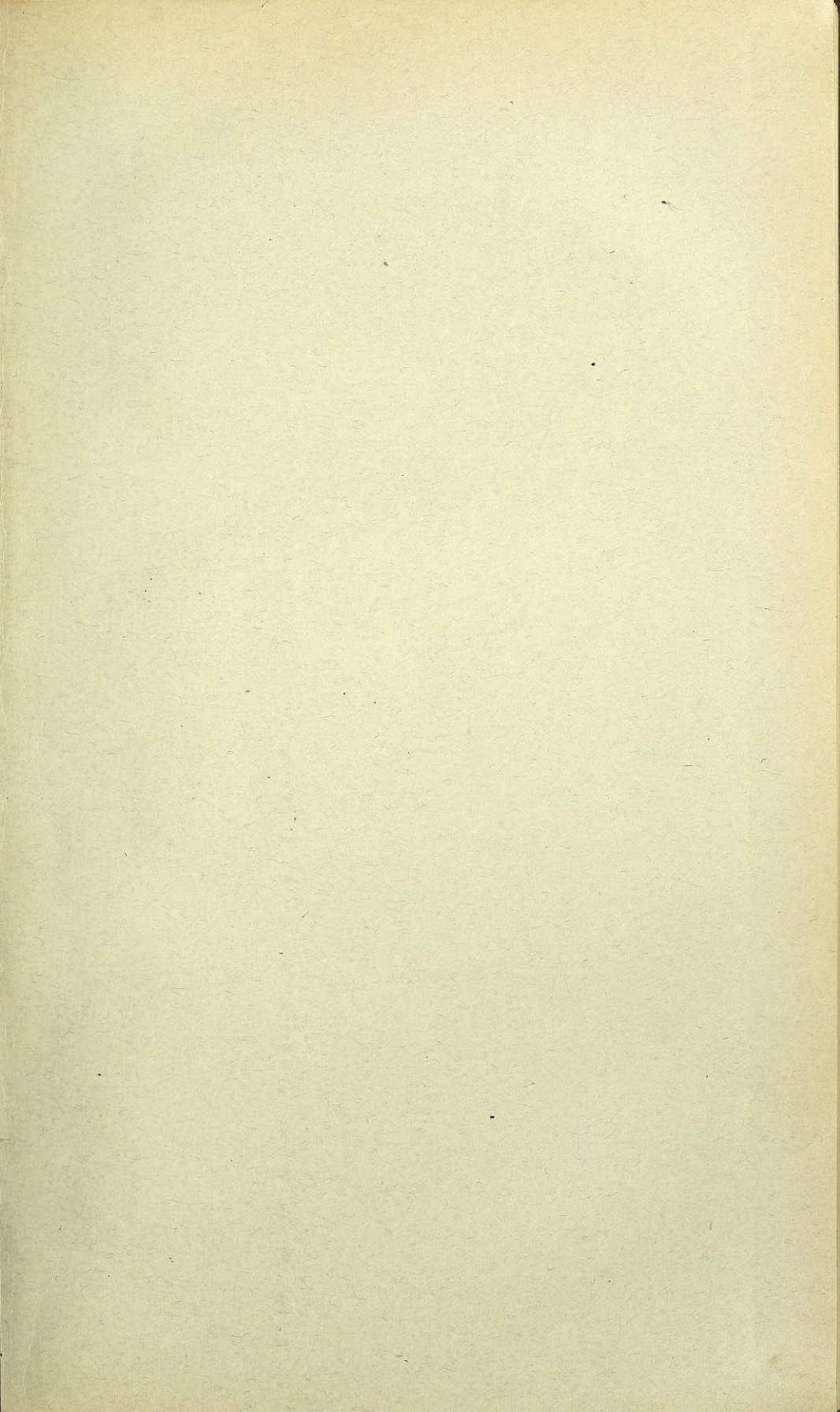
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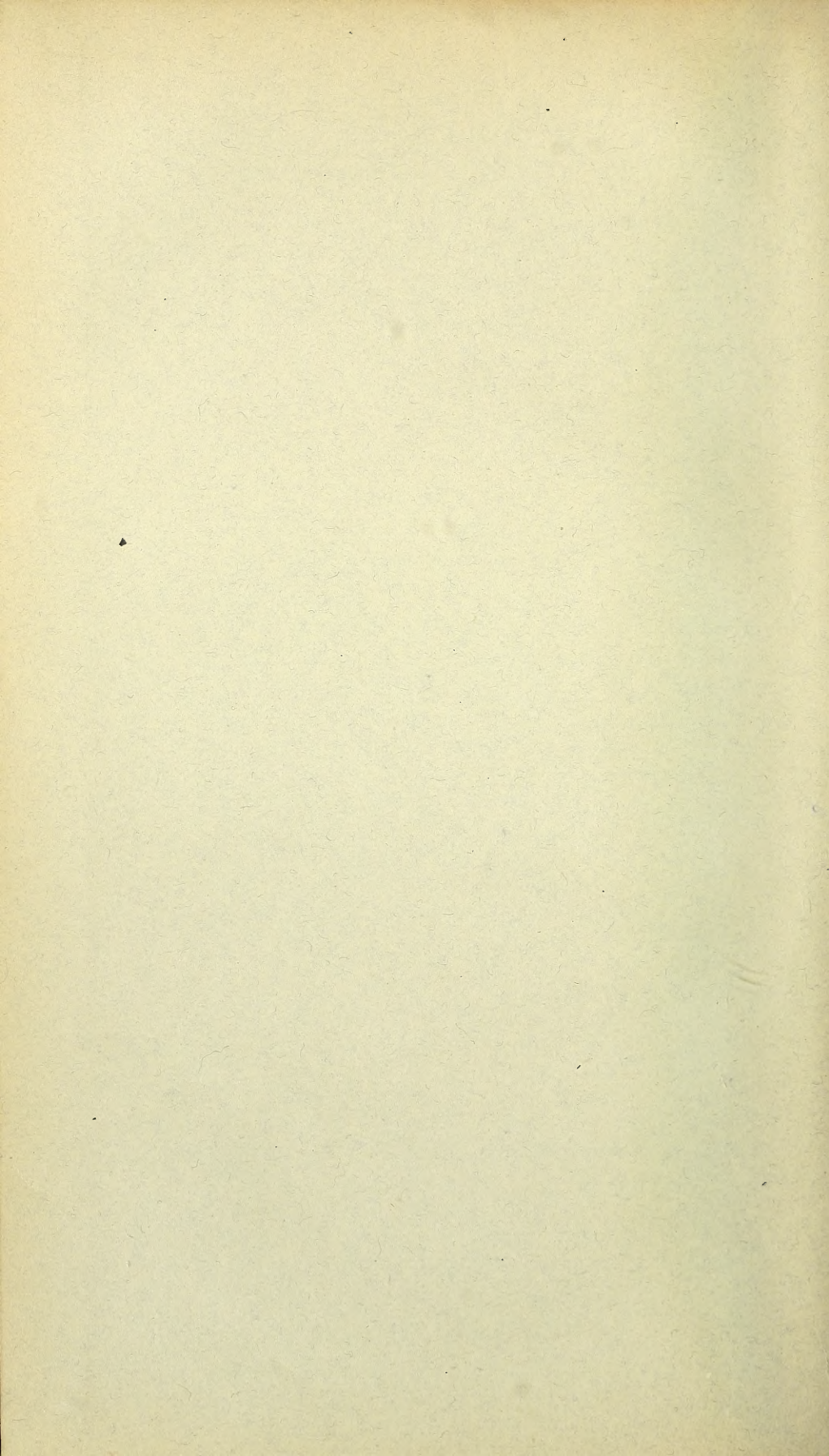
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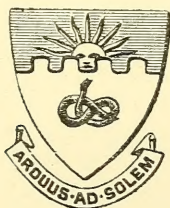
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BIOLOGICAL DEPARTMENTS

OF

THE OWENS COLLEGE.



VOLUME IV.

PUBLISHED BY THE COUNCIL OF THE COLLEGE

AND EDITED BY

PROFESSOR SYDNEY J. HICKSON.

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STUDIES

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The Editor wishes to express his sincere thanks to the Council of the Zoological Society of London, the Council of the Manchester Literary and Philosophical Society, and to the editors of the "Morphol. Jahrbücher," "Quarterly Journal of Microscopical Science," "The Annals and Magazine of Natural History," "The Annals of Botany," "The Liverpool Museum Bulletin," and of the "Ber. d. Deutschen Botanischen Gesellschaft," for permission to reprint the articles which appear in this volume.

P R E F A C E .

THE present volume of the Studies includes most of the papers that have been published by the workers in our Biological departments during the past four years, and it may be taken as a sign of our earnest endeavour to maintain the reputation of our laboratories as places of original research as well as of sound learning. In our opinion these two functions of such an Institution as this are inseparable ; but the demands made upon our time by heavy teaching responsibilities makes a continuous and systematic investigation of a definite subject a matter of considerable difficulty. The stimulus which the teachers of our departments received in previous years from the presence of the Bishop Berkeley Research fellows, whose whole time was devoted to original work, was most valuable. In the Preface to Vol. II. of this series the late Professor Milnes Marshall said these fellowships "promise to rank among the most successful and most characteristic features of Owens College Institutions."

Now that the fellowships cannot be offered any more we may again express our appreciation of the generosity of the anonymous benefactor whose assistance has borne such good fruit.

Biology is now left in our College without any fellowship or scholarship to enable a promising student to devote a year of his life to original investigation before commencing his career as a teacher or medical student, and our well-equipped Research laboratory has consequently to remain unoccupied during the greater part of the year.

We cannot help feeling that if these facts were more generally known some help might be forthcoming from those who realise what Biology has done and is doing for the development of rational methods of modern medical research.

It is probable that this volume of the Studies is the last of the series.

Original work will be carried on as usual in the laboratories, but by increasing the list of institutions and persons to whom we send separate copies of our papers as they appear, we hope to avoid in future the

necessity of reprinting them in a volume form. Works in exchange for the Milnes Marshall Zoological library and the library of the Botanical department will at all time be gratefully received.

We cannot allow this opportunity to pass without expressing our sense of the loss to Biological science by the death of our friends, Dr. Pollard and Mr. Hick. It was with a heavy heart that we read the proofs of their last contributions to Science.

SYDNEY J. HICKSON.

F. E. WEISS.

Owens College,

December 4th, 1899.

Reprinted from the "ZOOLOGISCHE JAHRBÜCHER Bd. VIII., ABTH.,
F. MORPH."

THE ORAL CIRRI OF SILUROIDS AND THE ORIGIN OF
THE HEAD IN VERTEBRATES.

By DR. H. B. POLLARD, *Berkeley Fellow in the Owens College, Manchester.*

With Plates I—II.

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INTRODUCTION.

Nearly four years ago, I found in the cellar of the Anatomical Buildings at Freiburg i./B. a number of Siluroids, which Professor Wiedersheim openhandedly placed at my disposal, and I then began

my study of the head in this group. Being, however, engaged on *Polypterus*, I did not actively investigate their anatomy till October, 1891. After Christmas of that year Professor Wiedersheim procured for me more material, through the kindness of Dr. Günther, of the British Museum, and Professor Möbius, of Berlin, and I wrote a short paper on their lateral line system, though I also investigated other parts of their anatomy. Proceeding then to the Zoological Station at Naples, to occupy the Oxford University table, my work on this group was again interrupted, since I wished to make use of opportunities of studying the development of the head in fish. At Naples, however, I also dissected quite a number of the more uncommon Selachii and Teleostei, and came to the conclusion that very little information could be gained as to the ancestral history of the head, from a study of its development.

Before leaving the Zoological Station I made the wax plates for a model of *Silurus glanis* from a valuable series of sections, which Professor Dohrn, knowing how widely my views differed from his, with generous magnanimity, handed to me for examination.

On my return to England I continued the present work at University College, London, where Professor Weldon supplied me with some specimens of *Myxine*. My study has been completed as Berkeley Fellow of the Owens College, Manchester. I am also greatly indebted to the Governing body of my Oxford College, Ch. Ch., which renewed a research scholarship. To the late Professor Milnes Marshall I owe a specimen of *Protopterus*, and to Mr. Hoyle, Keeper of the Manchester Museum, the opportunity of making a preparation of *Ceratodus*. In various museums I have taken every opportunity of studying fish, both recent and fossil.

The wax models described in this paper were made from the following species :

Auchenaspis biscutatus Geoffr., Cameroons.

Trichomycterus tenuis (*Pygidium tenue*) Weyenbergh, Sierra de Cordoba.

Callichthys paleatus Jenyns, Porto Alegre.

Silurus glanis.

A small specimen of *Chaetostomus guairensis* Steind., Caracas, was unfitted for modelling.

TECHNIQUE.

The models have been made after the well-known method of Born, but with certain additions to the technique. The heads of the small fish were decalcified in picric acid, stained with alum carmine, and subsequently with bleu de Lyon. Camera drawings were made on ordinary tracing paper and then rolled in with the wax to make the plates. I used the cheap impure wax with a low melting point of the kind used, I am told, by printers. A large rectangular museum bottle proved the best table on which to cut out the plates.

After reaching a certain size the models became extremely difficult to handle and it was necessary to find some method of strengthening them. I decided to electroplate them. The parts were wired together and then brushed with a suitable kind of blacklead. Then by applying in the copper sulphate bath, a current up to 5 or 10 ampères, according to the size of the model, a deposit of copper of sufficient solidity was formed in a few hours.

Subsequently they were painted and photographed. For opportunity of carrying out these operations I am indebted to the Physical Department of the Owens College.

By subsequent calculation I find that the models are an appreciable fraction too long in comparison with the breadth, but that does not detract to any great extent from their value. The wax plates must be made considerably thinner than the calculated thickness, but how much thinner depends on the "personal equation."

ON THE OCCURRENCE OF ORAL CIRRI.

Oral cirri, barbels, barbules or tentacles occur in many fish, and form one of the characters diagnostic of the Siluroids (*Nematognathi*), in which they occur throughout, with the apparent exception of *Plecostomus*. Much information on them can be gained from systematic works, especially from Günther's Catalogue of Fishes, where the subject is treated from the systematist's point of view.

True barbels do not grow out indefinitely, but only with certain morphological relationships, and the maximum number in the Craniata is 6, or perhaps 7 pairs, which I term nasal, premaxillary, maxillary, coronoid, mental (and extramental) and submandibular.

I attempted to draw up a list shewing the occurrence of the

individual tentacles, but had to relinquish it from lack of morphologically precise observations. These tentacles may be bifid and perhaps completely split, or fringed, but nevertheless all processes from the skin round the mouth, *e.g.*, those of *Plecostomus* may not be considered proper tentacles, though they may in a remote way have been connected with tentacles. Such skin processes may be compared with the fringe round a lamprey's mouth.

Tentacles occur in Cyprinoids, and especially in *Cobitidae*, where they attain an equal development with the Siluroids. They appear also in *Gadidae* and other fish. *Motella tricirrata* and *Mullus barbatus* are familiar examples. Again they are found in Sturgeons, as the barbels under the snout, and in the larva of an Amphibian, *Dactylethra (Xenopus)*.

Below the fish they appear in Myxinoids, and as I maintain, in the well-known form of the oral cirri of *Amphioxus*.

A typical tentacle should consist of the following parts: (1) a skeletal axis connected with a root piece, the axis being accompanied by (2) sensory nerves, which supply tactile organs in the skin, and worked by (3) muscles belonging to a special system and not homologous with the metameric body muscles, the (4) motor nerve supply being from nerves which have been shown to arise from the lateral cornu of the central nervous system, and to proceed out with the sensory nerves.

DESCRIPTIVE PART.

Model of Auchenaspis (Figs. 1, 2, 8).

The head of a specimen 5 cm in length, was cut in sections 30 μ thick. Every second section was drawn with a camera with a magnification of 28 (Zeiss Oc. 2, Obj. aa, height above table of drawing 19 cm). Thickness of wax plates 1.35 mm.

Model 23 cm long (or a little over 9 inches) by 20 cm broad.

The head as far as reconstructed was about the size of a hazel nut. The specimen was no doubt a young one. The replacement of cartilage by bone has not occurred to any great extent. The head was not modelled further posteriorly than the anterior semicircular canal.

The anterior semicircular canal is enclosed in cartilage, which does

not however extend up as a tegmen cranii, nor is it prolonged downwards to form the floor of the cranial cavity, and there is no appearance of resorption of cartilage, to indicate that at an earlier ontogenetic stage it extended further. A pterotic ridge is present, better developed in its posterior than in its anterior part, and it bears the moderately long articulation for the hyomandibular. The articulation is a very flat one, showing that there can be little movement of the hyomandibular on it.

In the cranial floor, two blocks of cartilage occur, at the level of the anterior semicircular canal. The cartilage of the auditory region is continued forwards as the wall of the orbital region, a bay in front of the anterior semicircular canal indicating where the facial and trigeminal nerves pass out. Slightly further forwards about the middle of the orbital region, the epiphysial bar (*Eph*) passes across the supracranial fontanelle, and somewhat further forward, there is a large open space in the cartilaginous wall. This is filled up by thin bone and does not transmit nerves or blood vessels. Below this a cartilaginous projection, directed backwards at each side of the pituitary body, forms a partial floor to the brain in this region. It leaves a deep notch below the orbital wall, filled up however by thin bone.

Where the orbital joins the ethmoid region, a slit-like preorbital canal (*Pr. orb. c.*) can be seen. It transmits a vein and the Ophthalmicus superficialis, VII. The nerve runs in a foramen of the cartilage on the right side of the drawing, the opening being seen from the front, on the preorbital process. On the left side of the figure, a notch corresponds to this foramen, the cartilage being partly replaced by bone.

The preorbital process is well developed, but not of great vertical extent.

An extraordinarily well developed rostrum is present, triangular in section in its anterior part, the upper angle truncated in the posterior sections. This rostrum extends far back posteriorly, as a thick cartilaginous septum between the olfactory nerves and lobes of each side, and from this septum a roof extends to the orbital wall and preorbital process, so that the olfactory nerves and lobes lie in long tunnels of cartilage, except where this is placed irregularly, above and below, by thin bone. In the model these replacements appear as asymmetrical open spaces on each side of the rostral region.

The anterior narrower portion of the brain case, that is, from the epiphysial bar forwards, is drawn out to a remarkable length, as indeed are all the structures of the anterior part of the head. The hyomandibular cartilage (*H.M.*) is triangular in form, the lower angle being produced into a strong process, which bears the operculum without the intermediation of an opercular cartilage. An extensive but thin block of cartilage (*Qu*) remains in the symplectic and quadrate region, and sends inwards and forwards a short pterygoid process.

The cartilaginous terminal portions of the prepalatine piece (*Prepal.*) are shown in the figures, the part round about the articulation with the preorbital process being replaced by bone. The prepalatine cartilage reaches almost to the tip of the snout. A small round block (*m.v.s.*) between the ends of the prepalatine cartilages in the model represents, in a very diagrammatic fashion, the premaxillary piece and rudimentary median support of the velum.

The Meckelian cartilage (*Mck*) has an inverted T-shape, the arms of the T being long. The posterior arm does not reach the quadrate, the quadrato-mandibular articulation being formed by bone. The upper process is the coronoid process (*Proc. cor.*) which bears the long and large procartilaginous coronoid piece (*Cor. p.*), which is continued into a tentacle combining characters of maxillary and coronoid tentacle (*Max. t.*), in that it is continuous with the coronoid piece, and also supported by the maxilla, which is attached to the end of the prepalatine cartilage. The tentacle is directed outwards and backwards. The anterior arm of the Meckelian cartilage is the mentomeckelian process (*M.mck.*), which is very far from reaching its fellow of the opposite side. I am inclined to think that it has not, at an earlier ontogenetic stage, extended further.

In the fleshy lower lip, there is a huge block of procartilage¹ (*Ment. p.*), with a projection directed posteriorly, while medially and somewhat below this block may be seen on each side the mental tentacle (*Ment. t.*), which is actually supported by a lamina of procartilage, lying superficially below the dentary bone. This supporting lamina is of considerable extent.

A submandibular tentacle (*Subm. t.*) lies below the coronoid process, also with a superficial supporting lamina of procartilage.

¹Better termed Extramental.

A stylohyal (*Sty. hy.*) bears the ceratohyal (*Hy.*) which is massive posteriorly. The thickened anterior end bears a hypohyal piece.

Model of Silurus (Figs. 3, 4).

Sections $15\ \mu$ thick. Every third section drawn, with magnification 28 (Zeiss Oc. 2, Obj. aa). Height of drawing above table 19 cm. Wax plates 1 mm thick. Model, reconstructed as far as middle of horizontal semicircular canal (on one side), 11 cm long and 15 broad.

The drawings for this model were taken from sections belonging to Prof. Dohrn, which he kindly allowed me to use. The cartilage was at its maximum development, no replacement by bone having occurred.

The skull wall, in the auditory region, is not completed on the internal aspect, but on the contrary, a large fenestra is left, as is the rule in Teleostei. The cartilage of the side wall of the cranial cavity only extends back so far as to separate the anterior semi-circular canal from the brain, while above, in the same region, a cartilaginous roof extends towards the middle line very slightly beyond the level of the membranous labyrinth. The pterotic ridge, which is on a level with the external semicircular canal, is not specially strongly developed. Below the pterotic ridge is the articulation for the hyomandibular, which is a long narrow articulation, situated at an angle of 30° to the median axis. From the pterotic ridge, the floor of the auditory capsule slopes, at an angle of 30° with the horizontal plane, to the basiscranial region where it is continuous across the middle line, behind the large pituitary fontanelle.

As is well known, an interorbital septum is never formed in Siluroids, and at this young stage the orbital walls are very wide apart. The upper portion of the orbital wall (Parker's supraorbital band) is a forward prolongation of the auditory capsule, and is triangular in section for some distance, the pterotic ridge being also continued forwards. The pterotic ridge can in fact be traced on to the antorbital process. In front of, and partly below the auditory region, is a great foramen in the skull wall, through which many of the cranial nerves pass out, all from the optic to the facial. This is partly filled, in the adult, by the so-called prootic. The floor of the cranial cavity is continuous cartilage, except for the large pituitary fontanelle, but, between this foramen and the pituitary fontanelle, the cartilage is much reduced in breadth and thickness. The skull wall in the anterior half

of the orbital region is complete and passes into the ethmoid region. At its anterior limit there is a foramen, the *Canalis praeorbitalis* (*Pr. orb. c.*). At the junction of the orbital and ethmoidal regions the epiphysial bar (*Eph.*) passes across the supracranial fontanelle, thus dividing the latter into pre- and post-epiphysial portions.

The side wall of the skull is produced into a large vertical antorbital process, separating the nasal and orbital cavities, and the cranium is almost as wide in this region as in the auditory region. At its antero-lateral extremity, the antorbital process has an articulation for the prepalatine piece (*Prepal.*). The nasal cavities are wide apart, the rostral portion of the chondrocranium being very broad. The olfactory lobes and nerves lie, as it were, in two short tunnels, being separated by a thick internasal septum and roofed over by the bridge of cartilage, which extends from the anterosuperior orbital region to the rostral region. Between the antorbital process and the base of the rostral region lies the extensive floor of the nasal cavity. The shape of the rostral region is best shown by the figure (Fig. 3).

The hyomandibular (*H.M.*) articulates, as above mentioned, with the pterotic region of the auditory capsule. Its upper portion is in the form of an inverted triangle, the articulation being the base of the triangle. At the apex of this triangular part there is a notch in front for the hyomandibular nerve, while behind is attached the opercular cartilage which bears the operculum.

From this level the hyomandibular cartilage broadens downwards and forwards to the quadrate and symplectic regions. At the posterior ventral angle, that is in the symplectic region, is attached the stylohyal, while at the most ventral, or quadrate region, is situated the articulation for the lower jaw. Inwardly and forwards, the quadrate is prolonged into the small pterygoid process, which in *Silurus* is attached by a ligament to the vomer.

The prepalatine piece articulates with the antorbital process. It is an irregularly shaped block of cartilage. In some specimens there may be found at its anterior edge accessory nodules of cartilage. Externally it bears the procartilaginous axis of the maxillary barbel (*Mx. t.*), which proceeds out at a right angle for a short distance, then turning backwards. The prepalatine piece has no connection with the pterygoid process.

In front of the rostrum is a small triangular block (*Pmx. p.*) representing somewhat schematically the premaxillary block of procartilage.

The Meckelian cartilage (*Mck.*) passes horizontally forward from its articulation with the quadrate. An angular process, however, passes downwards and backwards from the articulation. At some little distance forward, the coronoid process is given off. The coronoid process (*Proc. cor.*) projects vertically upward and bears the procartilaginous, cylindrical, horizontally placed coronoid piece (*Cor. p.*), which reaches forward to the level of the prepalatine piece, its end, in fact, approaching the maxillary tentacle.

Directly below the coronoid process lies the proximal portion of the submandibular tentacle (*Subm. t.*), and, some little distance in front of this, is seen the corresponding part of the mental tentacle (*Ment. t.*). Beyond the level of the mental tentacle, the Meckelian cartilage becomes distinctly more slender (*m. Mck.*) passing over continuously, in the symphyseal region, into the corresponding portion of the opposite side. Viewed from the front, the model reveals a most remarkable conformation of the edge of the rostral portion and the Meckelian cartilage, a bay being formed in the rostrum above, and in the Meckelian cartilage below. A nodule (*m. v. s*) attached to the rostral region, in the bay, represents a tentacle-like procartilage support of the upper "Velum," or flap used to close the mouth in respiration, and a corresponding nodule (*m. v. s*) on the Meckelian cartilage represents the lower tentacle-like support of the lower velum.

The stylohyal bears the enormous ceratohyal (*Hy.*) which is much expanded at its anterior and posterior ends.

The middle portion which is strengthened by perichondrial bone is thinner. Anteriorly are found the smaller hypohyals.

Model of Trichomycterus (Figs. 5, 9).

Specimen about 2.5 cm in length. Sections 20 μ thick. Every second section drawn with magnification 48 (Zeiss Oc. 14 Obj. aa.). Height above table of drawing 19 cm. Thickness of wax plates 1.6 mm. Model about 13.5 cm long by 18.5 broad. Reconstructed so far as to show the hyomandibular.

The head was about the size of a small pea. The replacement of cartilage by bone has gone on in places so far as to seriously interfere with the modelling although the specimen was very young,

the nerves being almost in an embryonic condition. Apparently in all the S. American Siluroids ossification begins at a remarkably early stage.

The auditory region shows much replacement of cartilage by bone, only irregular and asymmetrical projections being left. Cartilage only remains in fact in the neighbourhood of the hyomandibular articulation. A pterotic ridge is little developed and the hyomandibular articulation, which is very great in extent anteroposteriorly, may be said to be on the pterotic ridge itself. The cartilaginous floor of the brain case is only represented by three isolated blocks, one unpaired and median at the level of the auditory labyrinth, and a pair situated below the foramen of exit of the Facial and Trigemini nerves.

The supraorbital band is the only remaining cartilage of the posterior part of the orbital wall. It is somewhat triangular in section. At the middle of the orbital region the epiphysial bar (*Eph.*) passes across the supracranial fontanelle. In the anterior border of the epiphysial bar at the median point is a notch where the epiphysis rests.

In front of the level of the epiphysial bar a portion of the cartilaginous side wall is left and shown foreshortened in the figure (Fig. 5) but there is no antorbital process and no bridge above from the orbital to the rostral region (in other words the olfactory lobes and nerves are not roofed over by cartilage). The internasal septum takes the form of a distinct rostrum which however does not project beyond the level of the anterior narial opening.

In the cranial floor behind the rostrum is a pair of small fontanelles in the cartilage. One is indicated by the shading on the right of the drawing. These lodge minute projections from the base of the forebrain.

Behind the epiphysial bar the skull cavity widens out very remarkably. From the epiphysial bar forwards it is much smaller as shown in the figure. The hyomandibular (*H.M.*) articulates with the skull by an enormously long articulation and only along the articulation does much cartilage remain. There is, however, a strong process downwards and backwards which supports the operculum without the intermediation of an opercular cartilage.

Another block of cartilage remains in the symplectic and quadrate region, the intervening portion having been replaced by perichondrial bone.

A small pterygoid cartilage (*Pty.* Fig. 9) is independently formed much further forward. It may be seen on the left of the figure partly hidden by the prepalatine piece. The cartilaginous apophyses of the prepalatine piece (*Prepal.*) remain as a small portion at the articulation near the base of the rostrum and a large distal block.

Above the prepalatine cartilage is the nasal tentacle with a slight basal expansion. This forms the outer wall of the anterior narial opening.

The rostrum bears at its tip the upper tentacle-like support of the velum (*m.v.s.*). A small nodule of procartilage is seen on the left between the prepalatine and the velar supports. The maxillary tentacle (*Mx. t.*) does not rest on the prepalatine piece but is supported by the intermediation of the maxillary bone. Its base is bifurcated on the left side of the figure.

The Meckelian cartilage (*Mck.*) is represented as a triangular block. The posterior portion has undergone partial resorption and the posterior angle is far from reaching the quadrate. The upper angle is prolonged into a vertical somewhat anteriorly directed coronoid process (*Proc. cor.*) to which is affixed the procartilaginous coronoid piece (*Cor. p.*) which is large and passes continuously into the coronoid tentacle. The tentacle (*Cor. t.*) turns downwards, outwards, and backwards. The anterior angle of the Meckelian cartilage is produced into the mentomeckelian process (*m. Mck.*) which is short and very far from reaching its fellow of the opposite side. The distance of the mentomeckelian processes from each other is well shown in the figure.

A stylohyal cartilage (*Sty. hy.*) is present and bears the ceratohyal which is very thick at its two ends. In the specimen the middle portion was replaced by perichondrial bone on one side. The distal extremity bears a hypohyal.

The postero-ventral tip of the ceratohyal bears a procartilaginous prolongation (* Fig. 9) which supports the uppermost branchiostegal ray. It may perhaps be considered the homologue of one of the cartilaginous branchiostegal rays of *Selachii*.

Model of Callichthys (Figs. 6, 7, 10).

Specimen 3 cm. in length. Sections 25 μ thick. Every second section drawn, with magnification 28. (Zeiss, Oc. 2, Obj. aa). Height of drawing above table 19 cm. Wax plates 1.2 mm. thick.

Only the end of the snout reconstructed. The specimen was young but replacement of cartilage by bone has proceeded to a considerable extent, especially in the rostral region.

The median cartilage of the rostral region slopes sharply downwards and forwards, and, viewed from the side, its profile is curved. The floor of the nasal cavity extends laterally as two wings, actually prolonged still more laterally by the prefrontal bone. At the median anterior part of the rostral region there are abundant traces of resorption of cartilage, showing that a more distinct rostral prolongation was present at an earlier stage. This resorption is the cause of the irregular appearance of the anterior face as seen in the model.

Below the junction of the lateral and medial portions, a remarkable though slight projection of cartilage (* Fig. 7) bears the prepalatine bones, of which the large cartilaginous apophyses are seen in the figure, placed curiously close together and, along with the so called ethmoid bone, reaching very near to the tip of the snout.

Below and in front of the prepalatine cartilage is seen the three-rayed, procartilaginous premaxillary piece, forming the tip of the snout (*Pmx. p.*).

The maxillary tentacle (*Mx. t.*) is attached to the prepalatine cartilage through the intermediation of the maxillary bone. The tentacle itself passes sharply downwards and backwards, below the coronoid tentacle. Behind the maxilla lie the paired, external tentacle-like supports of the velum (*l. v. s.*).

Only the mentomeckelian portion of the lower jaw (*m. Mck.*) is seen in the model. A coronoid process is not developed, and the coronoid piece is only represented by a procartilaginous rudiment, not shown in the model. The coronoid tentacle (*Cor. t.*) proceeds backwards, almost parallel with the mentomeckelian cartilage, and it is fused with the distal portion of the mental tentacle (*Ment. t.*). The mental tentacles, which have a beautifully curved form, are fused with one another at their bases in the middle line, below the premaxillary piece. The junction is in front of, and slightly below the symphysis of the dentary bones.

The distal fusion of the mental and coronoid tentacles deserves especial attention.

Sensory Tentacular Nerves of Auchenaspis (Fig. 8).

The trigeminal nerve passes out from the skull, along with the Facial, in front of and below the hyomandibular articulation, thence passing downwards and forwards below and somewhat internal to the eye, which in Siluroids is small. Just below the optic nerve it divides into two great branches, the upper and internal shortly dividing into palatine (*R. Pal.*) and maxillary branches. The lower branch slightly further forwards divides into Ramus coronoideus and Ramus mandibularis.

The palatine branch, after separating from the maxillary, passes inwards through an anterior portion of the adductor arcus palatini muscle, that part which stretches from the skull wall in the anterior orbital region to the posterior end of the prepalatine piece, and which moves the maxillo-coronoid barbule. The motor nerves to this muscle run along with the palatine nerve. Reaching the skull wall the prepalatine nerve passes downwards and forwards, beneath and internal to the preorbital process, lying in fact beneath the lower wall of the passage of the olfactory nerves. Here it runs alongside the edge of the vomer and, reappearing in front of the postorbital process, proceeds, parallel to the edge of the rostrum and beneath the olfactory organ, to the end of the snout where, on reaching the premaxilla, it divides into several small twigs.

The maxillary nerve (*R. Mx.*) runs forward almost horizontally above the edge of the posterior part of the prepalatine piece, giving off the premaxillary branch and passing just outside the postorbital process. It then takes a long course forward between the anterior part of the prepalatine and the coronoid piece, giving off above a small branch to the skin and, below, another branch which supplies the skin at the base of the maxillo-coronoid tentacle.

The main portion turns outward and supplies the anterior face of the maxillo-coronoid tentacle.

The premaxillary branch (*R. pmx.*) passes external to the preorbital process, crossing over the prepalatine piece to lie internal to this piece, runs forward parallel to the edge of the rostrum, and divides into twigs which run beneath and outside the olfactory organs to supply the premaxillary region.

The coronoid branch (*R. cor.*) is given off from the mandibular nerve

and passes forward parallel to and just outside and below the maxillary nerve. It turns outward, still parallel to the maxillary nerve, and supplies the posterior face of the maxillo-coronoid tentacle.

The mandibular nerve (*R. md.*) passes downwards and forwards and, some little distance behind the coronoid process, it divides into Ramus mandibularis externus and *R. md. internus*.

The *R. md. externus* passes outside the coronoid process forwards and downwards outside the mento-meckelian process, and reaches the posterior edge of the mental piece (the large block of procartilage in the lower lip). Here it divides into a number of twigs which supply the fold of skin below and behind this piece.

The *R. md. internus* passes inside the coronoid process and divides into two branches which I name mental and submandibular. The mental branch (*R. ment.*) passes forwards, outside and below the mento-meckelian process, internal to the *R. md. externus*. Proceeding horizontally forwards, it crosses internally the block of procartilage of the lower lip and, reaching the mental tentacle, passes down it, dividing them into two branches, which supply the anterior and posterior aspects of the tentacle.

The submandibular branch (*R. subm.*), after parting from the mental, proceeds down outside the mento-meckelian process to the submandibular tentacle, dividing into two branches, which supply the anterior and posterior faces of the tentacle.

The *R. md. internus* contains motor portions, which pass off where the nerve divides into mental and submandibular branches, and supply, the anterior branches, the muscles of the mental tentacle, and the posterior the muscles of the submandibular tentacles.

More exact descriptions of the muscles and the motor supply must be reserved for a subsequent work.

I have not observed any ophthalmic branch of the Trigemini though some fibres may accompany the Ophthalmicus superficialis of the Facial.

Sensory Tentacular Nerves of Trichomyxerus (Fig. 9).

The Ophthalmicus profundus (*R. o.p.*) takes its exit from the cranial cavity independently of the maxillary branches, and is at first difficult to distinguish from the Ramus ophthalmicus superficialis of the Facial. It runs below the rectus superior, above the optic nerve, along the

wall of the orbital region, proceeding forwards, outside the olfactory organ, to reach the nasal tentacle, then dividing into two branches which supply this tentacle.

The great maxillary stem, taking its exit in front of the hyomandibular, proceeds downward and forward to below the eye. Behind the optic nerve it gives off the Ramus palatinus (*R. pal.*), which runs inwards and downwards, through the anterior portion of the adductor arcus palatini muscle (that part which moves the prepalatine piece and to which it gives motor fibres). Reaching the base of the skull it runs forward alongside the vomer and parallel to the edge of the rostrum, and then reaching the premaxilla it divides into several small twigs.

Below the eye the great maxillary stem divides into two branches the Ramus maxillaris (*R. mx.*) and the Ramus mandibularis (*R. md.*).

Almost immediately, the *R. maxillaris* gives off a Ramus premaxillaris (*R. pmx.*) which runs outside the anterior portion of the adductor arcus palatini, outside the articulating cartilaginous part of the prepalatine piece, above the bony portion, and internal to the anterior cartilaginous part of the prepalatine. Here it runs below the olfactory organ, parallel to the Ramus palatinus, and dividing into fine twigs, is lost in the tissue above the premaxilla at the tip of the snout.

The Ramus maxillaris runs forward horizontally, above and somewhat internal to the coronoid piece, dividing in front into three branches, the innermost of which supplies the skin internally at the upper anterior angle of the mouth, the upper and outermost branch passing downwards in front of the coronoid piece, then dividing into two twigs which supply respectively the anterior faces of the maxillary and coronoid tentacles. The third middle branch runs down, internal to the coronoid piece, and supplies the posterior face of the maxillary tentacle.

The Ramus mandibularis gives off a Ramus coronoideus (*R. cor.*) which runs forward, outside and parallel to the *R. maxillaris*, and turning down, proceeds to the posterior face of the coronoid tentacle.

The Ramus mandibularis, passing downwards, runs internal to the coronoid process and divides into mental and submandibular nerves, besides giving off motor fibres. The Ramus submandibularis (*R. subm.*) turns backwards, outside the coronoid process, and supplies the skin below the Meckelian cartilage, while the *R. mentalis* (*R. ment.*) is continued forwards to the front of the dentary region.

Sensory Tentacular Nerves of Callichthys (Fig. 10).

The main stem of the Trigemini passes below the eye giving off behind that organ a palatine branch, which divides into several small twigs supplying the roof of the mouth.

Below the centre of the eye the main stem divides into two branches, an upper and lower. The upper gives off shortly a Ramus premaxillaris (*R. pmx.*) and, as the Ramus maxillaris (*R. mx.*), runs forward along with the *R. premaxillaris* in a space between the adductor mandibulae and adductor arcus palatini muscles. The Ramus premaxillaris gives off small branches to the skin in the antorbital region and passes forward, lying near the skin outside the prepalatine piece, dividing into small twigs in the premaxillary region.

The Ramus maxillaris, running forward, divides into (1) a small branch which passes outwards and downwards and along the posterior face of the coronoid tentacle, (2) a large branch which runs down outside the maxillary tentacle and divides into four twigs, two of which supply the anterior and lateral face of the coronoid tentacle, and the other two the posterior face of the maxillary tentacle, (3) a branch which divides above the velar support, some twigs supplying the lateral part of the anterior region of the roof of the mouth, the remaining branch passing down inside the maxillary tentacle to supply its anterior face.

The Ramus mandibularis (*R. md.*) gives off a Ramus coronoideus (*R. cor.*), which is small and runs above and outside the adductor mandibulae muscle, turning down to supply the posterior face of the coronoid tentacle.

Continuing forwards and downwards, through the adductor mandibulae muscle, the Ramus mandibularis divides into *R. R. mandibulares externus* (*R. md. ext.*) and *internus*. The *R. mandibularis externus* lies outside the muscle and gives off a small branch, which runs downwards and backwards to the skin outside the Meckelian cartilage, thence, passing outside the anterior portion of the Meckelian cartilage, it continues forwards internal to the maxillary and coronoid tentacles, and reaching the mental tentacle, it divides into three small twigs, which supply the anterior face of this tentacle, the skin there being remarkably rich in sense organs.

The Ramus mandibularis *internus* divides above the Meckelian cartilage into *R. submandibularis* (*R. subm.*) and *R. mentalis* (*R. ment.*).

The former turns down outside the mentomeckelian process, while the R. mentalis continues on above it and passing forward horizontally, parallel to the R. mandibularis externus, divides into small twigs which supply the posterior face of the mental tentacle.

An Ophthalmicus profundus is only represented by certain fibres running in the course of the Ramus ophth. superficialis of the Facial.

Sensory Tentacular Nerves of Myxine (Fig. 11).

For purposes of comparison and in view of the object of this paper, I venture to give a figure of the terminal distribution of the sensory branches of the Trigemini in *Myxine*, with some description, though I have only one point to add to the almost perfect account given by Johannes Müller in his classical memoir.

In the figure the anterior part of the irregular nasal skeleton is shown, and supplying the skin in this region are several twigs belonging to one of the branches of the Ophthalmicus profundus (*R. o. p.*), the upper terminal branch of the first branch of the Trigemini of Müller, 5'' in his figures. One twig also proceeds to the premaxillary tentacle (shown in my figure with an asterisk).

The branch termed Ramus premaxillaris (*R. pmx.* in the figure) is Müller's "lower stouter branch of the first branch of the Trigemini, 5''." It runs alongside the premaxillary piece, the "vordere knöcherne Stütze der Schnauze," and, after giving off motor branches, supplies the first or premaxillary tentacle.

The above two branches form the "upper anterior branch of the Trigemini" and both are said to run above the optic nerve in *Bdellostoma*. They are by most authors termed ophthalmic branches, and I have kept that name in my preliminary communication.

The remaining branches belong to the "anterior lower branch" of Müller. The maxillary nerve (*R. mx.*) is his branch 6' and the coronoid (*R. cor.*) is his branch 6''. They supply the maxillary and coronoid tentacles.

My Ramus mandibularis (*R. md.*) corresponds to the "deeper finer branch, 6'', of the anterior lower branch." Only the sensory part is shown in the figure. It divides into a Ramus mentalis (*R. ment.*) supplying the fourth or mental tentacle, and a Ramus submandibularis (*R. subm.*), not specially mentioned by Müller, which supplies the skin

in front of and below the anterior lateral piece of the "Zungenbein" of Müller which I take to be the Meckelian cartilage.

COMPARATIVE PART.

Nasal Tentacle.

The most typical condition of the nasal tentacle is shown in *Trichomycterus*. The procartilaginous axis expands at its basal portion, and forms a partial wall outside the olfactory organ, being attached to a small bone, one of the terminal antorbitals of the series surrounding the suborbital branch of the lateral line system. This small bone and the base of the tentacle are supported by the prepalatine piece.

In *Clarias* the base of the tentacle is bifurcated, and the two prongs are attached to prefrontal and antorbital bones, at each side of the posterior of the nasal openings, the tentacle itself rising up in front of the opening behind the small nasal bone.

The position of the tentacle in relation to the anterior and posterior nostrils has been used as a diagnostic of certain groups of the Siluroids (Günther).

In *Motella tricinrata*, one of the *Gadidae*, far removed from the Siluroids, the procartilaginous axis of this tentacle bears the anterior tubular opening of the nose, and the basal portion forms the roof of the olfactory chamber.

In *Callichthys* though the tentacle is absent there is a procartilaginous roof to the olfactory chamber, which helps to support the anterior narial aperture and is obviously the basal portion of a tentacle.

Thus it is seen that when the tentacle is absent yet a basal portion of it may remain and form a support for the wall of the olfactory capsule. As such it is known to anatomists as the "nasal labial" or "Nasenflügelknorpel."

According to Sagemehl, such a nasal labial occurs in many Cyprinoids and perhaps in all; and also in the *Characinidae*. No doubt on special search it might be found in very many other groups of Teleostei.

The nasal labial of Selachii has been described in rich detail by Johannes Müller and Gegenbaur. Many references to such structures have been made by Parker, but subsequent investigation has shown his observations to be unfortunately unreliable.

In many Selachii the nasal labial is fused with the edge of the nasal

capsule, and indeed Gegenbaur concludes that it is a portion cut off from the cranium. That, however, is controverted by comparison outside the Selachii. In the Dipnoi there is a trelliswork of cartilage forming the wall of the olfactory capsule and, in view of the frequent fusion of the nasal labial with the cranium in Selachii, this trelliswork may perhaps be held to represent a nasal labial.

The nasal capsule and tube of *Myxine* is surrounded by irregular rings of procartilage, which represent the nasal labials. Gegenbaur, in mentioning this view, concludes that it is a hasty one, but all doubt seems to be removed by the fact that the nasal tube is worked by a muscle, the *Nasalis* of Fürbringer or "Zurückzieher der Nasenöffnung" of Müller, which belongs to the tentacular system and is supplied by the *Ophthalmicus profundus*, while the nasal tube itself receives sensory branches from the *Ophthalmicus profundus*. The compressor narium M. *ethmoideonasalis* F., and a portion of the *transversus oris* F. are also attached to the nasal tube.

On this point Müller remarks that "Since two olfactory nerves proceed into the single olfactory capsule, the single olfactory capsule is to be explained rather by the apposition than fusion of the nasal capsules of cartilaginous fish, and this happens indisputably through the suppression of those parts which otherwise lie between the nasal capsules". While agreeing with Müller in principle, I regard the supporting elements of the nasal capsule of *Myxine* as corresponding only to the nasal labial of Selachii, not to the whole capsule.

Furthermore no one, who has examined a series of sections of the head of *Myxine*, can doubt that the plate supporting the posterior part of the nasal or hypophysial tube where it opens into the palate, the "Gaumenplatte" of Müller or "posterior intertrabecula" of Parker is a posterior continuation of the nasal skeleton, and as such ultimately to be derived from a nasal tentacle.

Müller compared the nasal cartilages of *Chimaera* with the rings of the nasal tube of *Myxine*. This view is shown below to be untenable. Only the most anterior crescentic cartilage (*f* of Müller) corresponds to the nasal labial of Selachii and the nasal rings of *Myxine*.

Nerve Supply.

The motor nerves, which have occasionally to be referred to in this paper as supplying the system of tentacular muscles, are, to follow the

distinction established by His, nerves of the lateral cornu. The sensory nerves of the oral cirri are branches of the Trigeninus, and a sharp distinction must be drawn between them and the nerves of the lateral line system. The nerves of the lateral line system develop quite differently from the trigeminal branches. Their ganglia are derived from cells proliferating along certain tracts of the ectoderm as shown by Beard, Froriep, and Kupffer. I have followed the process myself in *Gobius*. The evidence of comparative anatomy is not less clear as to distinctness of the lateral line nerves in fish.

The topographical position and course of nerves is not of great importance. This has been determined by Stannius for the palatine nerves. "It is to be established that in certain classes of animals a larger, in others a smaller portion of allied elements may be contained originally in the course of one or other of two allied nerves, and at the same time the same elements may frequently arise by an indifferent root, without distinctly belonging to the one or the other nerve."

Numerous examples of this phenomenon will occur in this paper. The most extreme case is that of the premaxillary nerve of Myxinoids. According to Fürbringer the premaxillary nerve in *Bdellostoma*, runs over the eye-stalk and optic nerve, while in *Myxine* (and all other vertebrates) it runs below the optic nerve. Fürbringer indeed explains this by supposing the eye a later structure and capable of wandering, but an explanation on the grounds given by Stannius is more reasonable. Thus we see that the fundamental grounds for determining the homology of nerves are (1) origin from homologous nerve cells, (2) terminal distribution to definite structures. The course of the fibres is of less importance.

It is hardly necessary to remark, however, that an absolutely strict conception of homology is incompatible with a theory of evolution.

The sensory nerve of the nasal tentacle is the ophthalmicus profundus, and it is shown best in *Trichomycterus* where it takes the normal course of an ophthalmicus profundus, namely, below the rectus superior and obliquus superior, over the eyestalk. In *Trichomycterus* it runs on the outer side of the olfactory organ to reach the tentacle. In *Clarias* the nerve does not bear quite the same relation to the eye muscles, because the small eye, along with the muscles, is shifted very far laterally, while the nerve follows the skull wall more closely. It runs on the median side of the olfactory organ to reach the tentacle.

In other Siluroids the ophthalmicus profundus may only be represented by some fibres running along with the ophthalmicus superficialis of the Facial.

In some Siluroids e.g. *Silurus* (Stannius) and *Clarias* the trochlear nerve runs along with the ophthalmicus profundus. That is purely a case of apposition.

The comparative anatomy of the ophthalmicus profundus is fairly well known in the vertebrates, and need not be further entered into here, except as regards *Myxine*. In Cyclostomi, Müller and Stannius showed that it contains motor fibres, a fact of which most embryologists who have drawn up schemes of the head have been oblivious. The motor fibres supply muscles attached to and working the nasal tube and belonging to the tentacular system. Another feature in *Myxine* is that a small twig from the ophthalmicus profundus supplies the premaxillary tentacle.

Premaxillary Tentacle.

A premaxillary tentacle occurs in *Cobitidae* (*Misgurnus*) and some Cyprinoids e.g. *Barbus*, where it is attached to the premaxilla. However, these forms are much modified as to histology and topographical relations and are not suited to form a basis for comparison.

In Siluroids, though the tentacle itself is absent (except in *Aspredinidae* Günther), yet there is usually present a block of procartilage at the tip of the snout in relation with the premaxilla. In *Callichthys* (Figs. 6 and 7 *Pmx. p.*) this block is triradiate, occupying the tip of the snout below the prepalatine pieces, and on its lower surface develops the premaxilla. A corresponding block is present in *Chaetostomus*, differing somewhat in shape. With it articulate the anterior ends of the premaxillae which possess the remarkable form depicted by several authors in the *Hypostomidae*.

The ventral position of the mouth in these South American Siluroids is due to the large size of this piece and of the prepalatine, in addition to the presence of a rostrum. In Sturgeons it is due mainly to the rostrum, while in Selachii it is brought about by the position and size of the nasal capsules and the presence of rostral cartilages. In embryos of various vertebrates it is due merely to the mode of growth of the brain and olfactory organs.

In *Silurus* the premaxillary piece is represented by procartilage above and between the premaxillary bones. In many Teleostei it becomes a solid block of cartilage. It is mentioned by Stannius as a special part of the snout in front of the nasal septum. "In *Cottus* and *Belone*, a small discrete cartilage, applied to the anterior end of the skull, is covered by the premaxillae." "In *Malthaea* it forms a considerable free projection on the skull" (Stannius).

Sagemehl gave the rather unsatisfactory name "Rostrale" to this block and mentioned its existence in *Scomberesocidae*, *Cyprinodontidae*, *Scopelidae*, *Cyprinidae*, *Anacanthini* (*Macrurus*), *Acanthopteridae* and *Plectognathi*. "From its relations to the premaxillae we have every ground for the supposition that it originally formed the basis (Grundlage) of these bones. The fact that it occurs in far removed forms of Teleostei allows the conclusion that it is of great antiquity, and thus we may expect to find it in lower fish." "It is found in most distantly related groups, and this points to its being an inheritance from a very remote ancestral form."

Sagemehl goes on to compare it to a small cartilage between the ends of the palato-quadrate in *Heptanchus*. This view cannot be correct. Since it is unpaired the piece cannot, according to Sagemehl, correspond to a labial of Selachii. A premaxillary block also occurs in the Pharyngognathi (*Labrus*) and probably in many others not yet investigated, especially where the premaxillae possess a vertical upward projection, sliding on the ethmoid region. Among the older anatomists this piece has apparently also received the name prenasal cartilage, but I have not succeeded in running this term down.

An interesting feature in connection with this block is that the median velar support is shown by comparison to be a posterior prolongation from it serving to support the velum or fold of respiratory function, which lies behind the premaxillae. "In many Teleostei, mucous folds, placed behind the jaws, hinder the outflow from the mouth of the water which has been gulped in" (Stannius). The median velar tentacle-like structure is shown in *Silurus* and *Trichomycterus* (Figs. 3 and 5) and it occurs in many Teleostei. There may be also a lower median tentacle-like support of a lower velum, and these two give the appearance shown in *Silurus* (Fig. 3). It is the mode of development of these structures in the embryo which has given rise to the views of some embryologists on the paired nature

of the mouth of Teleostei. These structures possess no great morphological importance. A similar phenomenon is seen in the nose of *Myxine*, where a small process forms a partial septum in the nasal tube.

I propose to deal with the Selachii and some other forms later on.

In the Sturgeon, the most median of the two pairs of tentacles appears, from its nerve supply, to be the premaxillary tentacle.

The premaxillary tentacle of *Myxine* is the one which Müller showed to be the first, though viewed externally it lies inside and below the morphologically second. It is continuous with the unpaired bar of hard tissue, which underlies the nasal tube, and which is its root piece. Müller terms this premaxillary block the "knöcherne Stütze der Schnauze," and has given full details.

Nerve Supply.

Two nerves supply the region of the premaxilla. They are the palatine and a branch of the maxillaris, which I term here the premaxillary. The R. premaxillaris occurs throughout the Siluroids, with comparatively unimportant variations. In *Auchenaspis* it runs along with part of the buccalis.

The palatine nerve is also present in all Siluroids examined by me. It supplies the muscle which moves the prepalatine piece and, except in *Callichthys*, proceeds forward to the tip of the snout.

The R. premaxillaris corresponds to the nerve supplying the premaxillary tentacle of *Myxine*. This is usually considered to be an ophthalmic branch, and I have kept the old name in my preliminary communication. However, it is better to consider it a special branch, and not a mere portion of the ophthalmic. It is said to run over the optic nerve in *Bdellostoma*, and under it in *Myxine*, as in other vertebrates. It runs mainly in the substance of the palato-ethmoidalis superficialis muscle (Fürbringer) the Retractor of the bony support of the snout (Müller), outside the premaxillary piece, beyond which it gives off a motor branch to one portion of the Depressor of the mouth (U' of Müller). It then supplies the premaxillary tentacle, which also receives a twig from the ophthalmicus profundus.

Concerning the R. palatinus there are widely divergent opinions, which have been summarized by Stannius. In *Silurus glanis* he states that it is undoubtedly a branch of the Trigemini. In other forms it

appears to be Facial, and finally in "Ganoids," elements of the Glosso-pharyngeus enter into its composition (v. Wijhe).

Therefore, in considering its homologies, various components must be recognised in the palatine, and I consider the most anterior branches a dissociated portion of the R. premaxillaris. The most anterior tentacle of Cyprinoids is supplied by a nerve, of which Büchner has given a most excellent description (in *Barbus*). He terms it maxillaris superior. "It springs from the anterior internal border of the ganglion, passes in a canal formed by the upper convex face of the body of the sphenoid (parasphenoid) and the base of the greater (prootic) and lesser wing (orbitosphenoid) and is directed along the internal wall of the orbit, passes between the anterior frontal (ectethmoid) and palatine along the vomer and forms a kind of plexus with a branch of the maxillaris inferior (R. mx. superior). From this plexus start three branches for the two barbels and for the fleshy lip along the inter-maxillary. That of the superior barbel passes through a foramen, hollowed out at the internal extremity of the maxillary bone."

Sagemehl has described the nerve as palatine in Cyprinoids and agrees with Büchner, and I have myself followed the course of the nerve by sections and dissections in *Misgurnus fossilis*. It takes a course intermediate between those of the R. premaxillaris and R. palatinus of Siluroids, inasmuch as it passes below the prepalatine piece. I take it therefore, that this nerve almost universally termed palatine contains palatine and premaxillary fibres and corresponds to the Premaxillaris of *Myxine*.

The R. palatinus has been described in detail in the Sturgeon by Stannius and v. Wijhe, "In *Acipenser* the N. palatinus has relations really corresponding to those of Teleostei" (Stannius). "It runs forward along the lateral edge of the parasphenoid, separated from the orbit by a paired outgrowth of cartilage from the basis cranii. In front of this the nerve forms a network with the Ramus maxillaris superior, and then sends branches to the snout and ends in the tentacles" (v. Wijhe).

The barbels of Sturgeons are therefore premaxillary and maxillary tentacles.

Maxillary and coronoid Tentacles.

Maxillary tentacles are shown most typically in *Trichomycterus* and

Callichthys (Figs. 5, 6 and 7). They are supported, through the intermediation of a small maxillary bone (os labial Cuvier, adnasal McMurrich), on the prepalatine piece and extend downwards and outwards. They are also present in *Cyprinidae*. The coronoid tentacle is most typically shown in *Trichomycterus*, where it is very long. Its base passes continuously into a large procartilaginous root piece, the coronoid piece, which is firmly attached to the cartilaginous coronoid process of the lower jaw.

In *Callichthys* the tentacle is fused, near its base, with the mental tentacle, and the coronoid piece is only represented by a small mass of procartilage. The rudimentary tentacles of *Hypostomidae* are maxillary tentacles.

The tentacle at the angle of the mouth in the majority of Siluroids combines the characters of the two tentacles, and may thus be termed maxillo-coronoid. In *Auchenaspis* this is well shown (Figs. 1 and 2). The coronoid piece is seen to be continuous with the tentacle, but on the other hand this tentacle is borne by the maxilla, which articulates with the prepalatine piece. In *Silurus* (Figs. 3 and 4) the coronoid piece does not reach the tentacle actually, but approaches near it. What I think may be regarded as the proof of the fusion of maxillary and coronoid tentacles is given by the nerve supply. What occurs in the case of the mental and coronoid tentacle of *Callichthys* gives a clue as to how the fusion may have actually taken place. Judging from the nerve supply the outer pair of barbels of the Sturgeon are maxillary tentacles.

The prepalatine piece requires careful observation. In the young *Silurus* it occurs as a squarish block of cartilage, articulating with the preorbital process. In my specimen of *Auchenaspis* ossification had set in around the articulation, and consequently only apophyses of cartilage are left. The anterior block always lies very far forward in the snout. The posterior end serves for the attachment of the adductor muscle proceeding from the ethmoid wall. The muscle is mentioned by Stannius. It works the maxillo-coronoid tentacle. In *Trichomycterus* a small cartilage remains in the posterior part of the articulation, and on comparing closely the sections of the young *Callichthys*, I found that a small projection of cartilage from the skull represented this free cartilage of *Trichomycterus*. Thus we have a stage when the prepalatine cartilage is continuous with the skull cartilage (the spot is marked with an asterisk in Fig. 7).

In all Siluroids, this prepalatine piece never enters into continuity with the pterygoid cartilage, the latter being attached by ligament to the vomer. The lateral velar supports which may, as in *Callichthys* (Figs. 6 and 7) be of considerable size are apparently derivatives of the maxillary tentacle.

As to other Teleostei, Balfour remarks of the Salmon: "The anterior bar of the upper arcade is known as the palatine; but it appears to me as yet uncertain how far it is to be regarded as an element primitively belonging to the upper arcade of the mandibular arch which has become secondarily independent in its development; or as an entirely distinct structure which has no counterpart in the Elasmobranch upper jaw. The latter view is adopted by Parker and Bridge, and a cartilage attached to the hinder wall of the nasal capsule of many Elasmobranchs is identified by them with the palatine rod of Teleostei" (Prepal.). The development of this region in the Salmon has been worked out by Stöhr, who finds that tissue in the anterior trabecular region gives rise to trabeculae, palatine cartilage (Prepalatine), and tissue underlying the maxilla. The fusion of palatine and pterygoid elements occurs later. I have followed the process also in *Gobius*. It might be considered that these ontogenetic stages recapitulate the condition in Siluroids, but that can only be in a very limited sense, inasmuch as the piece in Siluroids is moveable, with special muscles, and does not bear any close resemblance at all to this embryonic condition. Indeed the resemblance is really closer in the adults.

In the Sturgeon free prepalatine cartilages exist, at any rate in the young animal, outside the basal angle (Basalecke) in front of the mouth. They may be the ethmo-palatines of Parker, but his lack of precision reduces the value of his observations. I cannot tell what Parker meant, since enthusiasm cannot replace accuracy. In *Polypterus* there is a separate ossification (autopalatine, v. Wijhe), in the upper jaw, where it articulates with the ectethmoid, and the cartilage projects forwards beyond this point. This is here called prepalatine. A similar projection occurs in *Chlamydoselachus* (Garman), so that, in this form, we must conclude that the prepalatine is really included in the jaw, in the region of the articulation with the preorbital process. In *Heptanchus* and *Hexanchus*, a posterior portion of the pre-palatine piece would appear to be represented by the "Lateral process of the ethmoidal region M," of Gegenbaur, which the latter homologizes with the "Schädelflossenknorpel" of Rays.

The second tentacle of *Myxine* is the maxillary tentacle. It lies outside and above the premaxillary and is connected by a bar of softer cartilage to the coronoid tentacle and to the antero-lateral piece of the tongue apparatus, the piece *W* of Müller and my *Mck* (Fig. 11). To the base of this tentacle, but not fusing with it, extends the process from the cranium, which Müller termed the cartilaginous process at the anterior end of the palatal ridges," the Processus spinosus of Fürbringer, or the Prepalatine of Parker.

The coronoid tentacle extends downwards and has an expanded root piece of hard cartilage. The prepalatine piece is in continuity with the ethmoid region, and thence with the subocular bar (Gaumenleiste of Müller), and the subocular bar is continuous with the auditory capsule and basilar part of the skull.

Müller makes the following remarks on the origin of the first cranium. On the fibrous membrane of the chorda tube arise paired cartilaginous rudiments of basilar pieces, running out into the auditory capsules and forwards as lateral wings. This is shown in *Ammocoetes* and *Myxine*. From this stage chondrification has proceeded further, and by various steps the condition of the chondro-cranium of higher vertebrates is attained. This is the simple view of Müller, and to me it seems still the most correct. Indeed where the conception of recapitulation in ontogeny has, in spite of the arguments of v. Baer, Gegenbaur and others, been introduced, there has often been great retrogression from the truth. Müller does not come to any conclusion as to the origin of the subocular regions and of the prepalatine piece. The prepalatine piece I regard as the root piece of a tentacle, and since there is no break of continuity in the skull of Myxinoids we may perhaps regard the subocular bar and "quadrate" regions as outgrowths and extensions of fused vertebral and tentacular elements.

This would mean that the autostylic condition of suspension of the jaws is the most primitive condition. To this conclusion I have come in a recent paper from quite different grounds.

The Labials (sensu strictiori).

Comparison of the traces of premaxillary, maxillary, and coronoid tentacles brings us to the question of the labials, as the term is strictly used by Gegenbaur. I shall treat of the subject rather in a historic way.

Cuvier (1814) dealt with the upper jaw of fish and came to the conclusion that the maxillary bones (labiaux ou mystaces) and intermaxillaries correspond to the two labials of *Squatina* and other sharks, while in the Rays the intermaxillaries are represented by the small cartilage in the nasal lobe, and the maxillaries by the "Schädelflossenknorpel."

On the maxilla of Teleostei he remarks: "Since the labial bone is unprovided with teeth in almost all the fish, it has little resemblance to the ordinary maxilla; but in order to be convinced as to its nature, it is enough to observe it in the trout or salmon, and thence to follow it in its various forms" (I may here remark that the Teleostean maxilla only partly corresponds to the maxilla of other vertebrates e.g. *Polypterus*, where it is mainly a "suborbital" bone.

On the Siluroids he remarks: "The intermaxillary, without a pedicle (ascending process), is situated under the anterior, more or less broadened edge of the skull and at each of its extremities is a small maxilla, which, becoming flexible, is prolonged into a long filament or barbel; in a word, the principal barbel of Siluroids is their maxilla prolonged." As to *Chimaera*: "In the thickness of the lip are found three bones (cartilages), which one recognises as the intermaxillary, maxillary, and the palatine arcade; this last is entirely suspended by muscles and ligaments, without articulating with anything."

Subsequent investigation has confirmed the remarks of Cuvier to a wonderful extent.

Rathke (1823) compared the labials of *Petromyzon* to the "Knorpelriemen" of *Amphioxus* (I quote from memory of the text).

Johannes Müller (1835) criticised Cuvier's accounts and views and attempted to show that the labials are structures not belonging to the general plan of the vertebrates, and that the upper jaw of sharks corresponds to the upper jaw of other vertebrates. "The tooth-bearing cartilage of Plagiostomi can be nothing else than the upper jaw (maxilla), while the labial bones are, as we have already shown, accessory pieces. Probably in the tooth-bearing cartilage, maxilla and premaxilla are united." The palatine arch of e.g. Teleostei is, according to Müller, represented by accessory cartilages in *Narcine* and other fish. Müller makes many valuable comparative observations, and gives a complete account and figure of *Callorhynchus*. His views have not met with acceptance, and have been abandoned since Hertwig's researches on dermal bones.

Gegenbaur (1872) gave a complete account of the structures in Selachii, accepting Cuvier's homology of the premaxillary and maxillary labials, drawing attention, however, to the distinction between the dermal bone and its subjacent tissue. The premaxillary bone must be imagined as developed phylogenetically, not from a cartilaginous substratum, but on such, the bone persisting while the cartilaginous substratum retrogrades and finally disappears. He then set forth his view that the labial arches are to be compared with arches of the inner visceral skeleton or branchial bars. This has been the basis for most of the modern German views.

Huxley (1876) compared the lower labials of the frog to the annular cartilage of the lamprey and the "incomplete ring" of *Amphioxus*, while the upper labials of the frog are the anterior dorsal cartilages of the lamprey.

Balfour (1882) says of the labials: "The meaning of these cartilages is very obscure; but from their being in part employed to support the lips and horny teeth of the Cyclostomata and the Tadpole I should be inclined to regard them as remnants of a primitive skeleton supporting the suctorial mouth with which, on the grounds already stated, I believe the ancestors of the present vertebrates to have been provided."

Howes (1891) has compared the labials of *Chimaera* and *Marsipobranchs*. His figures of Myxinoids are partly erroneous as to facts, being apparently compounded from museum preparations.

The question of the homology of the labials in *Chimaera* seems to me to be decided by the work of Vetter, the value of which can hardly be overestimated. He describes in detail the musculature of the labials in *Chimaera*.

These structures are worked by four muscles; the Musculi labiales anterior and posterior, and two portions of the Levator anguli oris.

The Labialis anterior is supplied by an anterior motor branch of the Trigemini and corresponds closely to a portion of the Copulotenticulo-coronarius muscle of *Myxine* (Fürbringer) the "Kopf U" des zweiköpfigen Herabziehers des Mundes" (Müller) which, as I have shown, is innervated by a branch from the premaxillary nerve.

The Labialis posterior is a portion of the Kopf U of Müller, and is supplied by a most posterior branch of the motor part of the Trigemini.

The portions of the Levator anguli oris are the Retractores tentaculorum of *Myxine*.

We have therefore in these labials remnants of premaxillary, maxillary, and coronoid tentacles. To put the homologies, which I maintain, into unmistakeable form, I will refer to Müller's figure of *Callorhynchus*. I take his "äusserer Nasenflügelknorpel *e*" to be the remnant of the premaxillary tentacle, his "oberer Seitenknorpel des Mundes *c*" to be a remnant of the maxillary tentacle, his "unterer Seitenknorpel des Mundes *b*" to be the coronoid tentacle, his "innerer Nasenflügelknorpel *f*" to be the nasal labial or remnant of nasal tentacle.

Then the remaining piece, the "Träger der Lippenknorpel und der Nasenflügelknorpel *d*" can only be the prepalatine piece, precisely as Cuvier maintained.

The labials of Selachii are then easily shown to be premaxillary, maxillary and coronoid tentacles.¹

Further, by comparison of Holocephali and Dipnoi it is rendered probable that the posterior upper labial of *Ceratodus*, as described by Huxley, and one of the antorbital cartilages of *Protopterus*, as represented by Wiedersheim and Röse, and other authors, are homologous with the prepalatine piece, and to proceed outside the limits of the fish, the "Cartilago labialis superior" of the Anuran tadpole, as shown in the splendid work of Gaupp, is also a prepalatine piece. In *Dactylethra* larvae it bears a maxillo-coronoid tentacle.

There still remain some few structures to be considered. Sagemehl has described certain small cartilages in the region of the articulation of the maxilla, which he terms submaxillaria, in *Catostomidae*, *Gymnotus* and *Perca*. He homologizes them with the upper labials of Selachii, giving, however, no figures, and adding that they correspond to the two small upper labials described by Parker in Salmon embryos, where always supposing Parker's figures to be correct, they belong rather to the premaxilla.

Then, also, there are the "Mundwinkelknorpel" referred to by Müller and Stannius. That of *Polypterus* is the coronoid labial, as it is attached to the coronoid process. In others more definite observations are needed to show whether these "Mundwinkelknorpel" are coronoid or mental pieces.

¹The lower labial of Selachii may, however, prove to be extramental, in which case the coronoid would be absent as a rule. In *Scymnus* there is a mass of soft cartilage along the upper jaw which might then represent the coronoid.

Certain muscles in Teleostei, considered by Vetter superficial portions of the adductor mandibulae, proceed, not to the lower jaw but, to the maxilla and neighbouring parts. The Adductor tentaculi of *Amiurus*, described by McMurich, is one of these. In *Cobitidae* (*Misgurnus*) they are very large, labial muscles also being present in correspondence with the presence of the tentacles. Vetter states that they are innervated by a special motor branch of the Trigemini. They correspond to the Retractores tentaculorum of Myxinoids, and are a further proof of the correctness of the views here maintained.

Nerve Supply.

It is impossible in Siluroids to sharply define maxillary and coronoid nerves, inasmuch as many fibres running along with the maxillaris supply the coronoid tentacle. However, there is always a coronoid branch arising from the mandibularis and supplying the posterior face of the coronoid tentacle. Where the coronoid and maxillary tentacles are fused, as in *Auchenaspis*, the branch is still present in exactly the same relation, and this, indeed, is one of the proofs that the maxillo-coronoid tentacle contains maxillary and coronoid elements. A similar coronoid branch is described as arising from the mandibular nerve in larval Salamanders, by von Plessen and Rabinowicz.

As to *Myxine*, the second branch of the Trigemini divides into maxillary and coronoid branches, apart from motor nerves. They supply maxillary and coronoid tentacles and the skin between them.

Stannius gives further descriptions of the distribution of the maxillaris superior in *Silurus* and *Acipenser*, mentioning the pre-maxillary branch in *Silurus*. He states that the maxillaris superior supplies the upper labial cartilages in *Spinax*.

Büchner figures the maxillaris superior in *Barbus* as an upper branch of the maxillaris inferior. He describes its course and its anastomosis with the premaxillary nerve (his maxillaris superior). The literature of the cranial nerves is immense, but I do not think the facts need further reviewing here.

Mental Tentacle.

The mental tentacles of *Callichthys* are fused at their bases, the fused portion lying medially in front of the symphysis of the dentary bones. Thence the tentacle curves down on each side, and, never

really becoming free to the exterior, fuses distally with the proximal part of the coronoid tentacle. There is no special root piece. In *Silurus* the mental tentacle is situated some little way back from the symphysis along the lower jaw, being supported by a plate of procartilage lying just internal to the skin. To this are attached muscles. The condition in *Auchenaspis* is similar, the basal plate being, however, very much larger. In *Auchenaspis* there is situated at the outside of the dentary bone a large block of procartilage (*Ment. p.*) with a posterior ventral projection running parallel with the tentacle as shown in Fig. 2. This block may be a derivative of the tentacle, possibly arising as a bifurcation of the proximal portion. Such a bifurcation is shown in the proximal part of the maxillary tentacle in *Trichomycterus* (Fig. 5, left side of the drawing).

The outer prong of the bifurcation may have expanded secondarily so as to have formed this great block. The outer mental tentacle of *Misgurnus* is a continuation from a corresponding block just as if the backward projection of the piece in *Auchenaspis* were prolonged into a tentacle. A corresponding piece is found in *Motella tricirrata*, and no doubt in many other Teleostei, in fact this may be in some fish the "Mundwinkelknorpel" of Stannius.

A median unpaired mental tentacle is also present in *Motella* and *Gadidae*, but it shows few of the characters of a typical mental tentacle. This tentacle is paired in *Mullus* and *Upeneus*.

The lower support of the velum may be a derivative of the mental tentacle though much modified. The mental tentacles of *Callichthys* show a remarkable similarity with the cartilage in front of the lower jaw of *Protopterus*, as figured especially well by Röse and of *Ceratodus* as figured by Huxley. I have, as in most cases, verified the observations myself, by sections in *Protopterus* and dissection in *Ceratodus*. This cartilage however passes under the lower teeth and is continuous with the Meckelian cartilage showing in this respect no correspondence with *Callichthys*. The position of this cartilage led Huxley erroneously I think, to term the lower teeth splenial.

The huge unpaired block of cartilage in front of the lower jaw in *Callorhynchus* is obviously a mental piece, corresponding to the mental cartilage of Dipnoi (lower labial of Günther), and somewhat doubtfully to the mental piece of *Auchenaspis*. In *Chimaera* as shown by Hubrecht and Vetter it is represented by a small pair of cartilages below the

coronoid labials at each side of the Meckelian cartilage. Howes has compared this mental piece with that of the Myxinoids and with the lower half of the annular cartilage of the lamprey, which Huxley homologised with the lower labial of the tadpole.

Considering now the Selachii, I have to withdraw a hasty statement in my preliminary paper that no traces of mental tentacles occur in them. Gegenbaur describes in a few Selachii small cartilaginous blocks below the Meckelian cartilage, and these he considers to be rudiments of rays showing that the lower jaw once bore a gill. In accordance with my theory I consider them to be the rudiments of the mental and submandibular tentacles. Gegenbaur goes on to make the far reaching suggestion that on such cartilages the jugular plates of *Crossopterygia* may have arisen. On my view the jugular plates would, like the premaxillae and maxillae, arise in connection with tentacles. However direct evidence is still wanting, unless indeed certain phenomena in *Ceratodus* may be interpreted as such. Huxley has described an ensheathing bone at each side of the symphysis, on the ventral face of the mandible. This he takes to be the dentary element, setting aside Günther's determination of the tooth as the dentary. The bone in question however lies in front of and below the mental cartilage, and may be interpreted on Gegenbaur's suggestion, as a paired anterior jugular plate. Jugular plates occurred in fossil Dipnoi but are usually stated to be absent in the living forms (Smith Woodward). This bone is absent in *Protipterus*.

The mental tentacle in Myxinoids is represented by a hard root-piece, bearing a rudimentary tentacle and suspended only by ligaments and muscles. It is fully described by Müller as the cartilage in the 4th or lowest tentacle.

Nerve Supply.

The nerve supply of the mental region is from the R. mentalis and the R. mandibularis externus. The Ramus mentalis in Siluroids runs outside or above the mentomeckelian process and forward, to run down outside the tentacle, where that is present, or to branch in the skin, when the tentacle is absent. The Ramus mandibularis externus may be a dissociated branch of the R. mentalis. It runs outside the coronoid process supplying in *Auchenaspis* the fold of skin below the mental block of cartilage. In *Callichthys* it is placed not so far forward.

Other details are given by Stannius.

In *Misgurnus fossilis*, the mental tentacle is supplied by a R. mentalis which crosses the Meckelian cartilage and then runs below that cartilage.

In *Motella tricirrata* the unpaired mental tentacle is supplied by a R. Mentalis which takes a slightly different course. It crosses the lower jaw rather far back, and then proceeds along with the R. mandibularis of the Facial, which supplies the mandibular branch of the lateral line system. This close apposition led Zincone to the erroneous view that the mental tentacle was supplied from the Hyomandibular nerve of the Facial.

The mental tentacle in *Myxine* is supplied by a mental branch proceeding forward as in Siluroids.

Addendum.—I must confess to not being able to speak with any feeling of certainty concerning the mental tentacle in Siluroids and Cyprinoids.

The independence of the R. mandibularis externus and the existence of the separate block in *Auchenaspis* may be taken to represent, as an alternative view to the above, a separate external tentacle or Extramental. Günther, in the Catalogue of Fishes mentions two pairs of barbels as occurring in a number of Siluroids close to the chin. This is also stated for *Cobitidae*, but I am in doubt whether the inner smaller process is a real tentacle or only a fold of the skin. It has the form of a tentacle.

The question may be decided by examination of fuller material or completer literature than has been accessible to me.

Submandibular Tentacle.

I have investigated the submandibular tentacle in *Auchenaspis* and *Silurus*. It lies just below the coronoid process, being supported by a subdermal plate of procartilage, which is very large in *Auchenaspis*. It has no typical relation with a root piece, but from careful comparison I am convinced that the Meckelian cartilage is the root piece of this tentacle, precisely as in the case of the premaxillary root piece, the prepalatine and the coronoid block. It is in *Myxine* that the Meckelian cartilage, or anterolateral piece of the tongue apparatus most closely resembles a root piece, a supposition strengthened by the disposition of the nerves. Occurrence of the submandibular tentacle is rare in fish.

The nerve supply is from the R. submandibularis which in Siluroids is given off from the R. mandibularis, just at the point of origin of the coronoid process. The Ramus submandibularis then crosses outside the mentomeckelian process to supply the tentacle. At the branching of the R. mandibularis into R. mentalis and submandibularis, the motor nerves to the muscles, moving the mental and submandibular tentacles are given off. A similar disposition of the nerves is described by Gaupp in Amphibia. "In Urodela and Reptilia, the principal portion of the Inframaxillary nerve runs in the canal of the lower jaw, as the Ramus alveolaris, forwards at the upper edge of the Meckelian cartilage, but a branch of this Alveolaris inferior runs down on the outer side of the Meckelian cartilage, and round its lower edge inwards, reaching the inner side after proceeding through a foramen (in *Siredon* between the dentary and opercular) and then supplies the Mylohyoid."

"This branch is the Ramus circumflexus, and in the Frog it alone forms the terminal portion of the Inframaxillaris." (Gaupp).

The R. submandibularis is present in Myxinoids, running, however, along with the mentalis outside the Processus coronoideus and supplying the skin in front of the Meckelian cartilage. This branch possesses a certain resemblance to the Ramus mandibularis externus but nevertheless it appears to me to be really the submandibular.

Meckelian Cartilage.

The Meckelian Cartilage of *Trichomycterus* is of an irregular inverted T-shape, the crossbar of the T being horizontal, the coronoid process representing the stem. The process towards the quadrate does not reach the articulation, partly because the cartilage, even at this young stage, has been resorbed after the formation of the os articulare. Probably at no ontogenetic stage was this arm at all massive. The mentomeckelian process is also very short and far from reaching the symphysis, that being formed by the dentary bones only. The Processus coronoideus proceeds upwards and forwards accompanied by bone. It bears the procartilaginous coronoid piece. The demarcation between the hyaline cartilage of the coronoid process and the procartilage of the coronoid piece is quite clear.

In *Callichthys* the coronoid process is wanting, and the coronoid piece is rudimentary. The mentomeckelian extends very little forwards

and to judge from the appearance of the cartilage there has been no resorption, so that probably it never extended further at earlier stages of its ontogeny. The mentomeckelian processes are as far from reaching the symphysis as in *Trichomycterus*.

In *Auchenaspis* the condition is a little different from that of *Trichomycterus*. The posterior arm is in the same state and the processus coronoideus passes up, and bears the coronoid piece. The mentomeckelian process is, however, longer, reaching halfway from the coronoid process to the symphysis, tapering away.

In *Silurus*, where the cartilage is more extensively present, the posterior arm extends beyond the articulation with the quadrate, as an angular process, and the mentomeckelian process is fused with its fellow and the symphysis. In *Hypostomidae* the whole rami of the lower jaw may be said to be free, there being no symphysis. A processus coronoideus is stated to be frequently present in fish by Stannius. "The lower jaw, varying to an extraordinary extent in shape, possesses often a special coronoid process." It is indicated in Dipnoi by the shape of the jaw, and the cartilaginous coronoid process can well be seen in sections.

The Selachii are not known to possess a coronoid process, the lower jaw in these animals being far from primitive.

It is no part of the present paper to follow out the coronoid process in the Vertebrates, and indeed complete observations on the relative extent of cartilage and bone are still wanting.

It may be remembered that the rami of the lower jaw of Teleostei are said to lie some way apart in embryos (Stöhr), but this may have nothing to do with the existence of the space between the mentomeckelian processes in Siluroids.

The anterolateral piece of the tongue apparatus in Myxinoids corresponds, to a certain extent, with the Meckelian cartilage. From its anterior upper corner a coronoid process proceeds to the coronoid piece and on to the maxillary tentacle, the relations in this respect being essentially the same as in *Auchenaspis*, where maxillary and coronoid tentacles are fused. The branches of the mandibular nerve run outside it however. No mentomeckelian process is present, or only virtually so, and there is no articulation with the quadrate region.

A number of muscles belonging to the tentacular system are attached to Meckel's cartilage. In Myxinoids the number is consider-

able. In Teleostei it is almost equally great, but in Selachii there has been much reduction and simplification. Vetter says of the adductor mandibulæ of Teleostei: "This muscular mass is nowhere found in the form of the relatively simple undivided adductor of Selachii or of *Chimaera* but always split into several portions. The Teleostei thus stand in regard to the jaw muscles much nearer to *Myxine* than the Selachii.

Many great authorities have held that the adductor mandibulae is the homologue of the adductores arcuum visceralium and that the jaws represent a visceral arch, yet this view appears to me to be entirely erroneous and to have turned subsequent investigations into a wrong path. In spite of the admirable researches of Johannes Müller, Fürbringer and Vetter, much remains to be done, especially in the way of comparison, since the muscles yield most conclusive evidence of the correctness of the Cirrhostomial theory.

The Cranium and other Parts.

Concerning the skull it is not my intention to enter into any great amount of detail. A cartilaginous tegmen cranii is not formed. However across the great fontanelle runs the epiphysial bar, beneath and slightly in front of which the pineal organ terminates. It divides the fontanelle into an anterior and posterior portion and the anterior part corresponds to the Selachian "Praefrontallücke" (Gegenbaur) inasmuch as a prolongation of the pineal organ is said to terminate at the anterior border of the tegmen cranii. Parker has described the tegmen cranii in the Salmon. An epiphysial bar is shown by Sagemehl in *Characinidae* and *Cyprinidae*. It is represented by a rudimentary block of cartilage, discovered by myself in *Polypterus*, and Gaupp has followed its development in the tadpole, terming it the *Taenia tecti transversalis*. The main fontanelle in the frog thus corresponds to the Praefrontallücke of Selachii. It is interesting to note that the cartilage follows the wandering of the pineal organ backwards, but the dermal bones do not, the pineal organ shifting from between the frontals to between the parietals.

There is considerable variation in the floor of the brain, cartilages remaining only as blocks or processes, paired or unpaired.

A preorbital process is not formed in *Trichomycterus*, but by various degrees it reaches a complete development as in *Silurus*.

One of the most remarkable features is the Rostrum or modification of the internasal septum. It is most marked in *Trichomycterus* and *Auchenaspis*. It becomes invaded by the so called dermethmoid bone. We have only to consider the rostrum somewhat prolonged to obtain a typical Sturgeon rostrum. The Sturgeons cannot be very far removed from the Siluroids, more especially the *Hypostomidae*, as indeed is suggested by Huxley's observations on the relation of the fossil forms.

The comparative anatomy of the hyomandibular is of very great interest, but, since I have already dealt with the subject in a paper on the suspension of the jaws, I need not refer to it in detail here. The hyomandibular articulates with the pterotic ridge by a long articulation. The immobility of the suspensorium of *Hypostomidae* is well known.

In *Clarias* the pterotic ridge is produced far outwards, the articulation of the hyomandibular lying some way from the cranial wall. The Siluroids approach near to an autostylic condition, or, to speak more correctly, are little removed from it.

HISTOLOGY OF THE TENTACULAR SKELETON.

I venture to give the following sketch of the varieties of cartilage present in the tentacular skeleton.

Condensed embryonic tissue, known as procartilage, develops in various directions. It may give rise to an intercellular matrix with a tendency to become refractile. Such a tissue, for the sake of comparison, I term soft Myxinoid tissue (A), inasmuch as it forms the axis of the tentacles of *Myxine*. The nuclei and protoplasm may disappear, and the intercellular matrix become very hard, as in the hard tissue of *Myxine*.

On the other hand the intercellular matrix may become fibrillar and the cells and protoplasm degenerate as in the tentacles of *Clarias* (B). Or the procartilage may develop into hyaline cartilage (C) or persist to a considerable extent in its embryonic condition (D). The refractile matrix is stained blue by Bleu de Lyon, while the nuclei and protoplasm remain unstained. The core of the tentacle may attain very little development, the tentacle then being very flexible, as in *Misgurnus*, or, on the other hand, as in *Motella* it may be formed by structureless bone, with a layer of osteoblasts round it. I have drawn

up the accompanying scheme of the occurrence of these tissues. A stroke between two letters indicates that the tissue is intermediate between two varieties.

	<i>Na.</i>	<i>Pmx. t. & p.</i>	<i>Ms. t. & Prepal.</i>	<i>Cor. t. & p.</i>	<i>Mental t. & p.</i>	<i>Subm. t.</i>
<i>Clarias</i>	B		B	C	(degenerate)	
<i>Auchenaspis</i>			B	C	A	B
<i>Trichomycterus</i> (young)	C/D		C/D	C	A	
<i>Callichthys</i> (young)		D	C/D	C	C/D	D
<i>Chaetostomus</i> (young)		A/D	A/B	C		A (hard)
<i>Acipenser</i> (young)		D	D	C		
<i>Misgurnus</i> (young)		(rudimentary)		C	D	Extramental D
<i>Motella</i> (young)	D			C	(replaced by bone)	Extramental D
Other forms		C		C	C/D	C
		(Teleostei)			(Polypterus)	(Dipnoi)

From such a scheme it may be learnt that all parts are independently variable. Root piece and tentacle in *Amphioxus* are essentially similar in structure. In Myxinoids the root piece is differentiated from the tentacle by the great development of the intercellular matrix, the hardening of the same, and the degeneration of nuclei and protoplasm. In Siluroids much more complicated differentiations have arisen. The tentacles are not of similar histological nature in different families. The root piece differs from the tentacle in the same individual, the root pieces differ among themselves, some being of procartilage, some of the Myxinoid tissue, and some of true hyaline cartilage. Usually in one animal all the tentacles are of similar histological nature, but nevertheless this is not always the case, *e.g.*, in *Motella tricirrata*.

To a certain extent the grade of histological differentiation is a measure of the constancy of the piece. For example, Meckel's cartilage and the hyoid cartilages occur in all the Craniata. The prepalatine piece, the hyaline premaxillary piece of Teleostei, the mental piece of Holocephali and of the Dipnoi are less omnipresent, but still run through whole orders, while less differentiated tentacles are present or absent in different genera. Of course there is no universal rule.

In view of the extraordinary amount of variation in histology and structure, it is very remarkable that, when tentacles do occur sporadically, they can be referred to certain of definite 6 or 7 pairs. Following the conception of Wiesmann, it would seem that the archi-

texture of the germ plasm is more constant than the quality of the determinants. Exceptions to this rule may be discovered.

The embryonic development of the tentacles in *Ictalurus albidus* has been investigated by Ryder. Those present in the adult develop early in situ, and there is no parallelism with the phylogeny.

REVERSION AND LARVAL FORMS.

From comparison of long lists illustrating the occurrence of the individual tentacles, and from consideration of the fact that they appear sporadically, I have come to the conclusion that it would be extremely rash to maintain that the tentacles have come down in unbroken ancestral line from an early progenitor. In other words, their presence must often be due to reversion.¹ They are not always the most primitive and archaic forms that possess the tentacles most fully developed.

All parts of an organ may not revert to the ancestral condition, or in other words the reversion may be only partial. Such is the case in the tentacles of *Cobitidae* where the skeletal axis is not developed. In the language of Weismann the reversion in this case is due to determinants in the skin, the skeletal determinants not being evolved.

When once a structure has arisen by reversion and been rendered constant by natural selection, it will develop ontogenetically direct to the adult condition, and therefore it is useless to seek for information as to its ancestral history in its embryological history.

It will I think be obvious, to anyone fully acquainted with the writings of Darwin and Weismann, that reversion may occur at any free living stage. Larval forms are often supposed to represent ancestral or existing adult forms. The resemblance has no doubt been greatly exaggerated. For instance I am not aware that *Ammocoetes* shows any approach in positive characters to *Myxine* or *Amphioxus*.

Nevertheless such characters as the prepalatine piece of tadpoles, and the maxillo-coronoid tentacles of the larva of *Dactylethra* at its fancied "Siluroid" stage, have to be accounted for. Tentacles do not

¹Or, in many cases, inasmuch as rudiments of tentacles are almost always present, by "re-development from rudiments" (Darwin). No sharp distinction can be drawn between the phenomena of reversion and re-development from rudiments.

occur so far as I know in other tadpoles nor in the larvae of Urodeles. Therefore probably we have here a case of larval reversion, but it is only an exceedingly incomplete reversion.

THE ZOOLOGICAL POSITION OF SILUROIDS.

The Siluroids are mostly freshwater fish with an extraordinary diversity of habits and structure and with a remarkably wide geographical distribution. While however the group as a whole occurs in all the zoogeographical regions, yet certain families are confined to one. Thus, for instance, the *Loricarina* with peculiar anatomical features appear to be confined to the rivers of S. America. (Certain forms from the oriental region have been allied with them by some ichthyologists.) They are freshwater forms without any means of passing across seas, being heavily armoured with feeble powers of swimming, lying at the bottom of pools in the daytime, and creeping about at night on banks by means of their strong spines, and feeding on soft substances more or less putrified (Weyenbergh).

We are justified by the principles of geographical distribution in attributing to *Loricarina* an antiquity like that of *Lepidosiren*.

Nor is there any reason, as far as distribution is concerned, for denying to other families, such as the *Clariina*, an immense antiquity. They are a now flourishing group, while the Dipnoi, with restricted range are a decadent group.

The dermal skeleton of *Hypostoma* and *Callichthys* has been exhaustively investigated by Hertwig, who found that their dermal teeth are homologous with the placoid scales of Elasmobranchs. Therefore the dermal skeleton must be regarded as exceedingly primitive. From that of *Hypostoma* may be derived that of *Acipenser*, which, however, is considerably more modified. Recently Klaatsch has attempted to upset Hertwig's conclusions, but I am not alone in thinking that in spite of the technical excellency of Klaatsch's work, he has signally failed to prove his point.

Another feature of considerable interest is revealed by the oral teeth of *Hypostomidae*. Some forms have been excellently figured by Kner. I would specially refer to his Fig. 1, Tab. 5.

The bent hook-like teeth of the premaxillary and dentary bones all converge in the same direction, and the two premaxillae and the two

dentary bones are separate, thus forming four independently moveable blocks. Such teeth can only be used for hanging on to some object.

Weyenbergh remarks "the fragility of these teeth is enough to show that the fish cannot use much force with them, and this is not necessary, because these fish feed on more or less putrescent organic substances. I have met, for example, with many specimens round a dead horse, which was decaying in the river Primero. It seems to me that their mode of feeding does not deserve the name of mastication, but rather of suction." It is of no little importance to find that these archaic animals have a suctorial mouth. Possibly the symphysial teeth of *Coccosteus* may also have been used for hanging on. No doubt *Coccosteus* did not live on dead horses, but even in palaeozoic times, there can have been no lack of decaying organic matter.

Coccosteus also possessed normal teeth in its jaws, so that it would appear to have been able, not only to hang on, but also to bite in the usual fashion.

The Siluroids are almost throughout characterised by having a very small gape of the jaws. They will suck at bait and not swallow it suddenly like ordinary fish.¹ Along with this is associated the fact that the suspensorium possesses little mobility and the suspension is little removed from autostylism, which I hold to be the primitive condition.

Of late years it has become customary to look upon the "Ganoids" as derived from Selachii, while the Teleostei are regarded as a flourishing offshoot from the least primitive of the Ganoids, *Amia*.

When the Ganoids were established as a limited group by the weight of Müller's authority, and further when the primitiveness of Selachii was so strongly insisted on by Gegenbaur, it was but logical to assume that a Selachian form gave rise to a Ganoid, and this in turn to a Teleostean.

However, the Ganoids are now being given up as a natural group.

Sagemehl's work illustrates the progress of such views. This author directly compared *Amia* with Selachii, and came to the conclusion that a form like *Amia* might be descended from an early *Notidanus*-like shark. Then he proceeded to show that the *Characinidae* are closely allied to *Amia*, while a group including Siluroids, *Gymnotidae*, *Chara-*

¹This information I owe to my friend, Mr. E. T. Mellor, who has observed the habits of Australian species.

cinidae, and *Cyprinidae*, must be founded under the term Ostariophyseae, since they possess in common the remarkable "Weber's apparatus." No weight can then be assigned to characters of the dermal armature or fins. Bridge and Haddon, also working on Weber's apparatus, seem also to accept the modern origin of Siluroids.

Thus, according to Sagemehl, the Siluroids are to be derived from *Amia*. Such a view seems to me inconsistent with all known principles of comparative anatomy and geographical distribution.

Any discussion on the affinities of the Siluroids would be incomplete without reference to the paleontological evidence.

Agassiz classed the Siluroids, on account of their dermal armature, with the Ganoids, from which they were removed by Johannes Müller. Subsequently (1858-61) Huxley following up the investigations of Pander, compared certain of the Siluroids with *Cephalaspidæ*. "No one can overlook the curious points of resemblance between the Siluroids, *Callichthys* and *Loricaria*, on the one hand, and *Cephalaspis* on the other, while in other respects, they may be still better understood by the help of the Chondrostean Ganoids." "I am inclined to place the Cephalaspids provisionally among the Chondrostei, where they will form a very distinct family." Ray Lankester at the conclusion of his monograph on the *Cephalaspidæ* remarks: "It cannot be too strongly asserted that these fishes are, as far as can be seen, by no means of a low type. At the same time there is nothing in the remains known to us which will indicate even approximately their affinities to any one of the large groups recognised in the classification of Amphirhine fishes." "The series of scales or bones along the body of *Cephalaspis*—so strongly recalling the cinctures of *Callichthys* which has a complete endoskeleton—are, probably, morphologically of the same nature as those structures, but anteriorly I have not been able to detect any modification of the flanking 'scales' in *Cephalaspis* in the form of clavicular bones." "It is best then to let the group of *Cephalaspidæ* stand alone."

Pander, Huxley, and Ray Lankester are therefore agreed that the dermal armature of *Loricarina* is like that of the oldest known vertebrate fossils.

Claypole (1892) has discovered Crossopterygian fins along with a Pteraspidian, *Palaeaspis*.

As to the Silurine forms, Huxley compared *Coccosteus* with *Clarias*

and concluded that the structural coincidences in the two forms "must lead us to assign a place near, if not among the Siluroidei to *Coccosteus*."

This view has not met with general acceptance and Traquair writes "Undoubtedly, the weakest point in Professor Huxley's 'Essay' is the attempt which he made to show by comparison of the exoskeletal plates of *Coccosteus* with the bones visible on the exterior of the skeleton of many recent Siluroids, that there was a possibility at least of the enigmatical group of the Placodermata turning out to belong to the great order of Teleostei, or ordinary bony fishes, 'hitherto supposed to be entirely absent from formations of palaeozoic age.' Recent discoveries in the palaeozoic rocks of America point, as we shall presently see, to another, and, perhaps more probable solution of the question."

The "perhaps more probable solution" is given by the discovery of *Dinichthys*. Newberry discovered that *Dinichthys* has a dentition like that of *Protopterus*, and therefore concludes that it is allied to the Dipnoi. *Dinichthys* being also allied to *Coccosteus*, it follows that *Coccosteus* is allied to the Dipnoi.

Nevertheless, too much stress must not be laid on a single feature. Fusion of teeth to form great dental plates has occurred over and over again in the Vertebrates as for example in *Plectognathi* and in *Hatteria*. The jaws of *Dinichthys* have far less resemblance to those of the more archaic *Ceratodus*, where the teeth lie on the inside on the lower jaw, than to the more modified *Protopterus*. Therefore, the resemblance may be due to convergence. Other features forbid entirely the close alliance of *Dinichthys* and *Protopterus*. The latter has no structures corresponding to the spines of the former. The whole dermal armature is entirely different, and finally the distribution of the lateral line system, as figured by Clappole, is in no respect like that of *Ceratodus* or *Protopterus* (I have examined both of the latter animals on this point), while it bears a remarkable similarity to that of *Clarias*, as figured by me.

Returning to *Coccosteus*, I may state that I have examined a number of specimens and the dermal armature certainly shows no affinity with Dipnoi. Elsewhere I have endeavoured to prove that the lateral line of *Clarias* closely resembles that of *Coccosteus*, thus offering confirmation of Huxley's view.

The Siluroids are therefore not classed with the *Cephalaspidæ* and

Coccosteidae mainly on negative evidence, such as the absence of pectoral fins or clavicular bones and the absence of internal ossification.

Owens College, Manchester,
Dec. 1894.

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LETTERING OF FIGURES.

<i>Cor. p.</i> Coronoid piece.	<i>Pr. orb. c.</i> Preorbital canal.
<i>Cor. t.</i> Coronoid tentacle.	<i>Prepal.</i> Prepalatine cartilage.
<i>Eph.</i> Epiphysial bar.	<i>Proc. cor.</i> Processus coronoideus.
<i>H. M.</i> Hyomandibular.	<i>Pty.</i> Pterygoid cartilage.
<i>Hy.</i> Hyoid.	<i>Qu.</i> Quadrate cartilage.
<i>l. v. s.</i> Lateral tentacle-like support of the velum.	<i>Sty. Hy.</i> Stylohyal.
<i>Mx. t.</i> Maxillary tentacle.	<i>R. cor.</i> Ramus coronoideus.
<i>m. v. s.</i> Median tentacle-like support of the velum.	<i>R. md.</i> Ramus mandibularis.
<i>Ment. p.</i> Mental piece.	<i>R. md. ext.</i> Ramus mandibularis externus.
<i>Ment. t.</i> Mental tentacle.	<i>R. md. int.</i> Ramus mandibularis internus.
<i>Mek.</i> Meckelian cartilage.	<i>R. mx.</i> Ramus maxillaris.
<i>m. Mek.</i> Mento - Meckelian process.	<i>R. ment.</i> Ramus mentalis.
<i>Na.</i> Nasal cartilage.	<i>R. o. p.</i> Ramus ophthalmicus profundus.
<i>Na. t.</i> Nasal tentacle.	<i>R. pal.</i> Ramus palatinus.
<i>Op. c.</i> Opercular cartilage.	<i>R. pmx.</i> Ramus premaxillaris.
<i>Pmx. t.</i> Premaxillary tentacle.	<i>R. subm.</i> Ramus submandibularis.
<i>Pmx. p.</i> Premaxillary piece.	

Plates I., II.

- Fig. 1. Model of *Auchenaspis*, front view.
 Fig. 2. " " " side view.
 Fig. 3. " " *Silurus*, front view.
 Fig. 4. " " " side view.
 Fig. 5. " " *Trichomycterus*, front view.
 Fig. 6. " " *Callichthys*, front view.
 Fig. 7. " " " side view.
 Fig. 8. Sensory branches of Trigemini of *Auchenaspis*.
 Fig. 9. " " " " " *Trichomycterus*.
 Fig. 10. " " " " " *Callichthys*.
 Fig. 11. " " " " " *Myxine*.



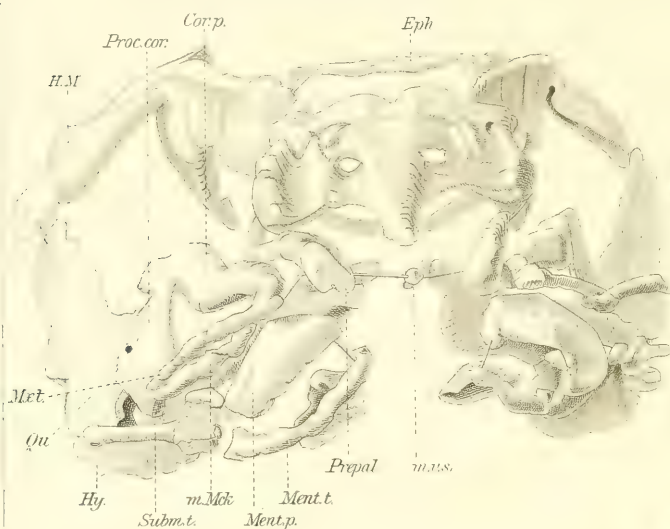


Fig. 1.
Auchenaspis.

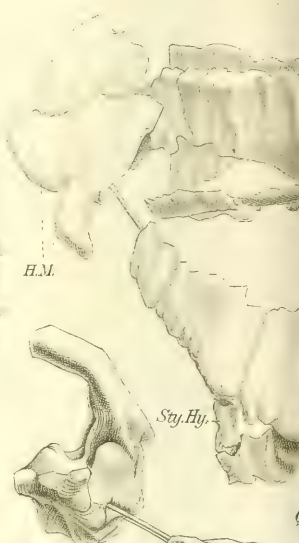


Fig. 7.
Callithys.

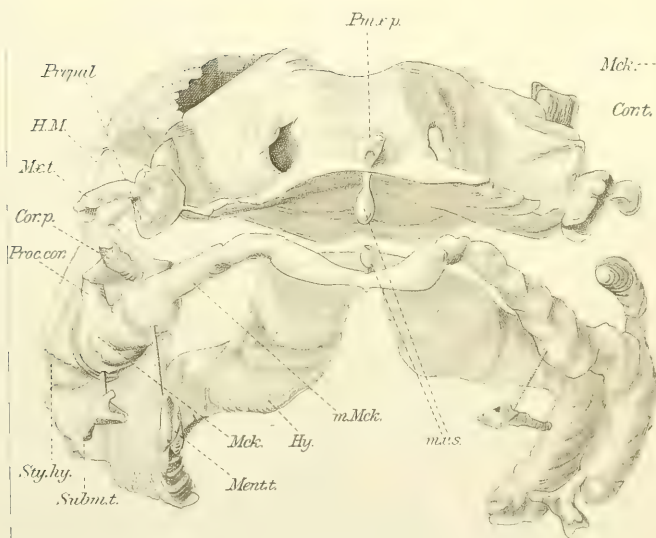
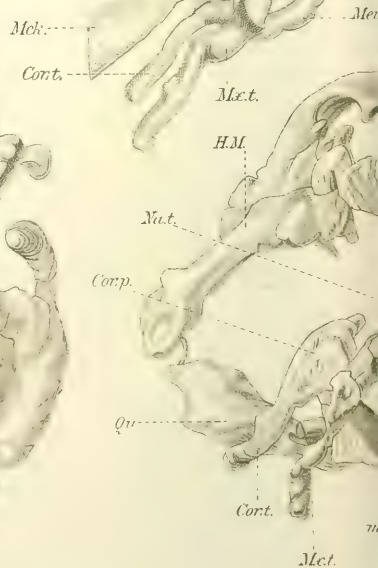


Fig. 3.
Silurus.



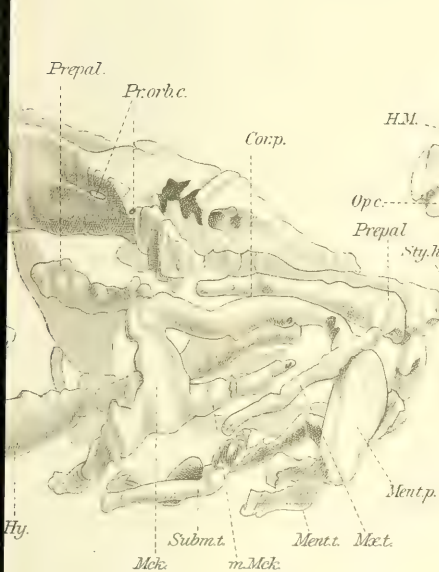


Fig. 2.
Auchenaspis.

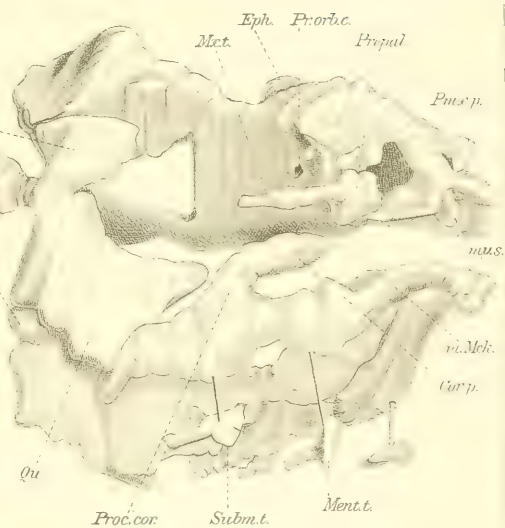


Fig. 4.
Silurus.

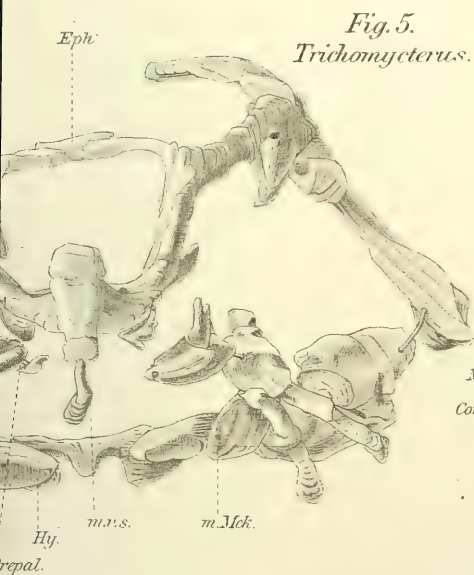


Fig. 5.
Trichomycterus.

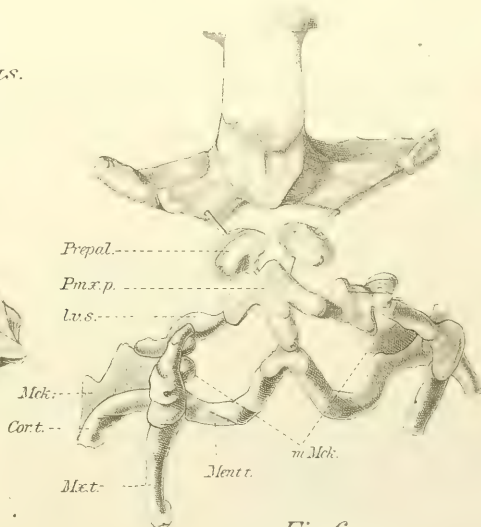
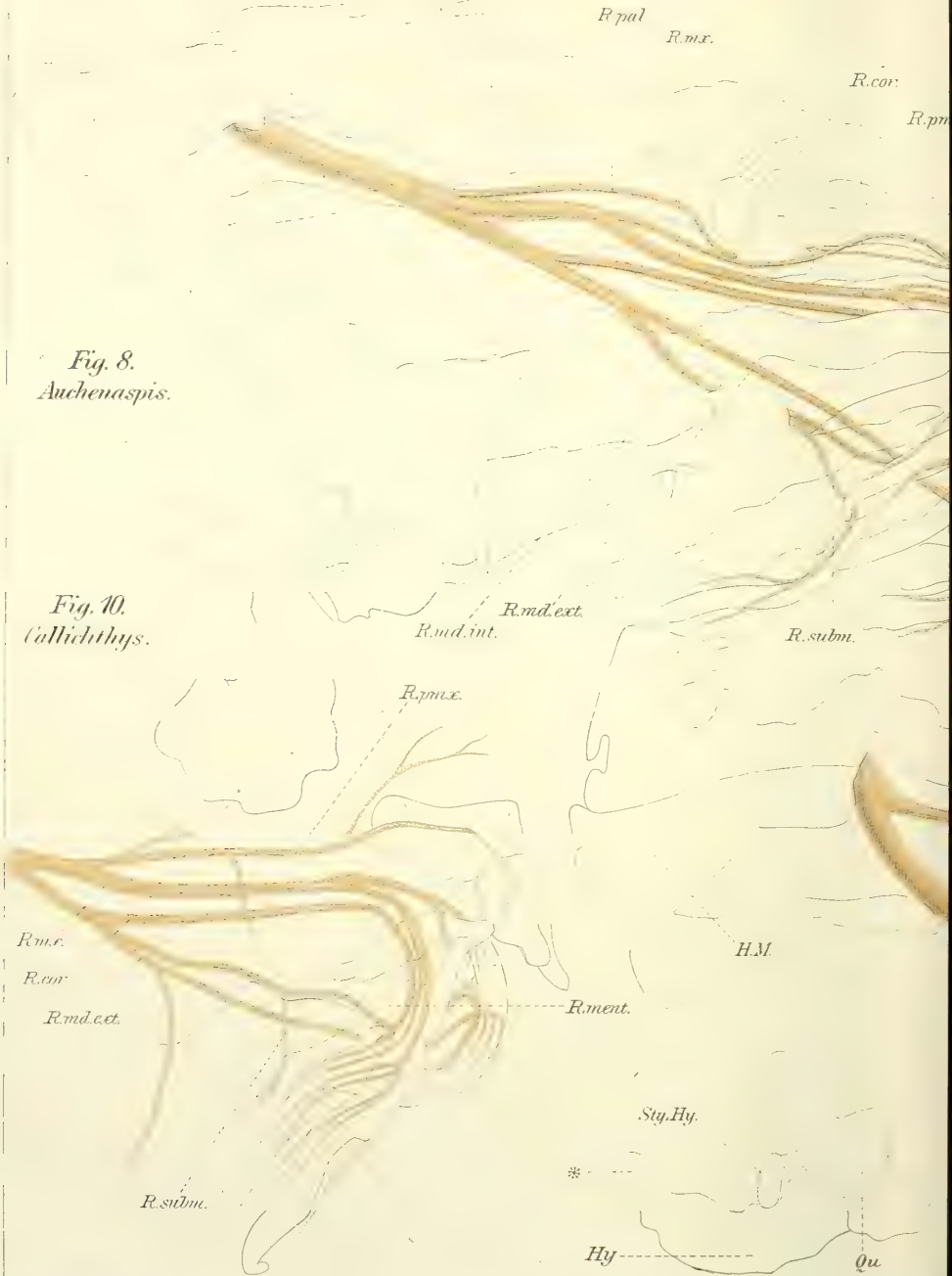


Fig. 6.
Callichthys.

Fig. 8.
Auchenaspis.

Fig. 10.
Callichthys.



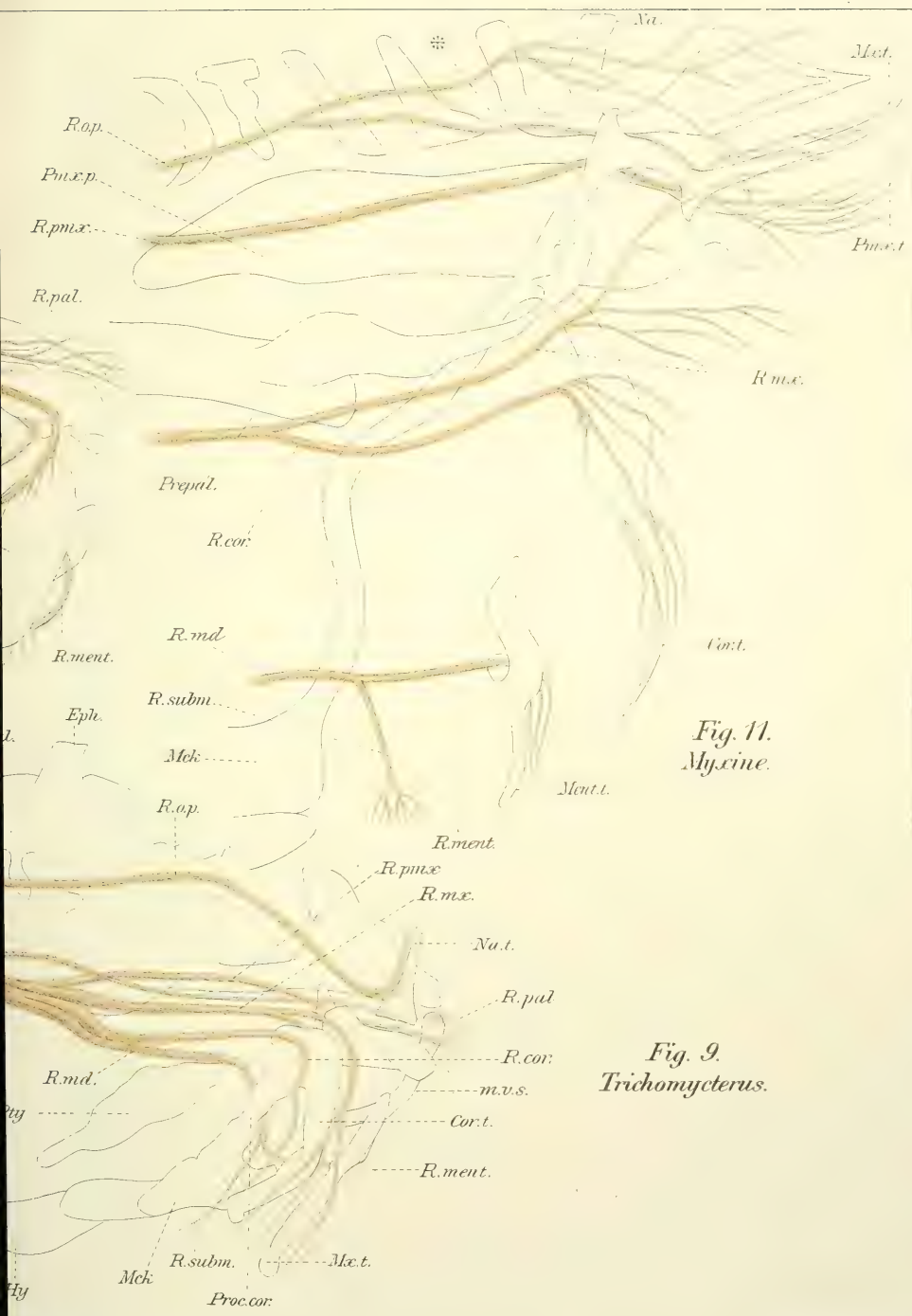


Fig. 11.
Mycine.

Fig. 9.
Trichomycterus.

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ON THE STRUCTURE AND CONTENTS OF THE TUBERS
OF ANTHOCEROS TUBEROSUS, TAYLOR.

By J. H. ASHWORTH, B.Sc.

In the Synopsis Hepaticarum (Gottsche, Lindenberg et Esenbeck, 1847) the occurrence of tubers in *Anthoceros tuberosus*, *Riccia vesicata*, *Riccia tuberosa* and *Petalophyllum Preissii* is mentioned.

The tubers of *Anthoceros tuberosus* were first described by Taylor in the *London Journal of Botany* (1846, p. 412), the specimens described being collected by Drummond on the banks of the Swan River in Western Australia. This account is quoted in the Synopsis, where the oval tubers are described (p. 792) as occurring chiefly, but not exclusively, in sterile plants, being formed at the ends of out-growths from the thallus, and containing a farinaceous mass within a deeply coloured envelope or cuticle. Attention is drawn to the presence of rootlets upon the tubers, and the latter, which are to be regarded as gemmæ, are said to serve as organs which can resist drying during the hot period of the year.

In *Riccia vesicata* (Taylor), the tubers are described as oblong or round and provided with rootlets (loc. cit. p. 795).

In *Riccia tuberosa* (Taylor), the tubers are described as pale yellow, rounded or oblong, slightly curved bodies, provided with rootlets, and yielding, on compression in water, a small amount of farinaceous matter and opaque globules (loc. cit. p. 796).

Nothing is said about the tubers of *Petalophyllum Preissii* (Gottsche) beyond the statement of their presence (loc. cit. p. 792).

Recently Goebel¹ has found tubers on a *Fossombronia* (n. sp.) from Tovar, which he finds are produced by the thickening, and filling with

¹ Flora. 1893. Band 77. G. Ruge. Beiträge z. Kenntniss der Vegetationsorgane der Lebermoose. p. 305.

reserve food materials, of a downward-growing apex, on entering the soil. In these tubers, Ruge (loc. cit. p. 306) finds that the reserve food materials contain considerable quantities of starch.

Beyond these observations I have been unable to find any other references to the tubers of Liverworts.

The object of my investigation was to ascertain the structure and the nature of the contents of the tubers of *Anthoceros tuberosus*. Unfortunately, I have had at my disposal only dry herbarium material, but I have been able to make out several new points of interest.

Anthoceros tuberosus. The tubers occur on the ventral surface of the thalloid expanse, and they lie embedded in the soil beneath the thallus. They are spherical or pear-shaped, their diameter being $\cdot 15$ — $\cdot 35$ mm., and the length of the stalk attaching them to the ventral surface of the thallus $\cdot 2$ — $\cdot 35$ mm. (Pl. III., Fig. 1). The wall of each tuber is formed of three or four layers of more or less rectangular cells, which are almost devoid of contents, there being only very small remnants of protoplasm found in some of the cells (Fig. 1, C). The walls of these cells are corky in nature, as they are coloured yellow by iodine, and are not swollen or turned blue by a subsequent treatment with strong sulphuric acid. Many of the cells of the outermost layer, and some of the cells of the stalk, are produced into hair-like processes, attaining a length of $\cdot 25$ mm. (Fig. 1, H.). These do not appear to be cut off by a cell wall from the cells from which they arise. The walls of these hairs, and also of the cells of the basal part of the stalk, differ slightly in composition from the corky cell walls, as on treating with iodine and sulphuric acid they stain slightly bluish-green, but do not swell appreciably. These cell walls appear to be cellulose which has become almost transformed to cork. The hairs are probably the remains of absorbing organs (the rootlets mentioned in the Synopsis) which performed some function during the formation of the tuber.

Within the protective cells, lie closely-packed cells, all of which contain food materials. The cell walls of this portion of the tuber are thin, and of unchanged cellulose (Pl. 2, Fig. 2). Each cell contains a large, central, usually elongated nucleus (N), a large number of colourless or slightly yellow round or oval granules (G), imbedded in the remains of the protoplasm (P), and numerous small oil drops (O), or one large one due to the coalescence of the smaller drops.

The oil is present in considerable quantity, as can readily be seen on crushing a tuber in water between a glass slide and a cover, when large fluid oil-drops exude. These are at once stained brown, or black, by osmic acid. The drops are readily soluble in chloroform, ether, benzene, but dissolve only slowly in absolute alcohol. The oil is not vaporised by heating for two hours to 120°—140°C., and it is not readily saponified with potash, even on heating for several minutes. The oil-drops are fluid at the ordinary temperature (12°C.), as can be seen on compression.

The granules present in the cells are of different sizes (Fig. 2); a few are large, but the greater number are of smaller size. The larger granules have an average diameter of .006 mm., the diameter of the smaller granules being about .002 mm. Both larger and smaller grains contain one, two, or three brighter and more refringent portions, which may be enclosed bodies or only specialised portions of the substance of the grains. The grains are swollen and dissolved by a weak solution of potash (2%), and in some grains there is an inner portion which remains undissolved for a short time. The granules are *not* starch, as they are stained *yellow* by iodine. They give other reactions for proteids; *e.g.*, they turn bright yellow when treated with nitric acid and ammonia (xanthoproteic reaction), and they stain readily with picrocarmine hæmatoxylin, aniline blue, acid fuchsin, and other protoplasmic stains. The tests mentioned above prove that the grains consist of some proteid substance, and they appear to be aleurone grains.

The food material stored up in the tubers of *Anthoceros tuberosus* differs, therefore, from that in the tubers of *Fossombronia* (n. sp.), which were found by Ruge to contain considerable quantities of starch. In the Synopsis, the tubers of *Anthoceros tuberosus* are said to contain a *farinaceous* mass; but it is necessary to remember, in considering this statement, that the nature of aleurone grains was only discovered in 1855, that is eight years after the publication of the Synopsis.

The small size of the granules in the tubers of *Anthoceros tuberosus* does not preclude the possibility of their being aleurone grains, as in some plants aleurone grains attain a diameter of only .001 mm. The occurrence of larger and smaller grains in the same cell is also known in other cases (*e.g. Vitis*). The occurrence of oil and aleurone grains together as reserve food materials is not at all uncommon, but they

have not hitherto, to my knowledge, been found together in Liverworts, though oil-containing bodies have long been known to occur in them.¹ The oil found in these tubers closely resembles that which Pfeffer found in other Liverworts in its solubility in various reagents, its fluid condition at a temperature of 12°C., the difficulty experienced in its saponification with potash, and in the fact that the oil is not vaporised on heating to 140°C.

Besides these stalked tubers projecting ventrally into the soil, there are analogous structures formed in the substance of the thallus, which have not hitherto been described. These are produced by the formation of a cellular mass (like that of the inner part of a stalked tuber) between the upper and lower layers of the thallus. The cells of these tuberous masses have the same structure and contents as those in the inner portion of the external tubers. These cellular masses are usually oval in shape, and their average length and breadth are .2 mm. and .15 mm. respectively. They are somewhat flattened dorsoventrally, their thickness being .1—.15 mm. In several sections, I have found one of these internal masses at the base of the stalk of an ordinary (but small) tuber. This suggests that, possibly, the stalked tuber in question was in process of formation, and that the cells at the base of the stalk were storing up food materials, which would subsequently be passed into the tuber. Internal masses of considerable size occur in other places in the thallus where there is no sign of the formation of a stalked tuber, and these probably always remain in the thallus, and are independent of any external tuber.

Regarding the function of the tubers, the Synopsis says they should be looked upon as gemmæ, and Ruge (Flora, 1893, p. 306) suggests that this process of vegetative reproduction is an adaptation to a mode of life in which the plants are subjected to periodic droughts. In support of this view he mentions the fact that the four plants which bear tubers, mentioned in the Synopsis, come from Western Australia. We may regard these tubers as gemmæ, the inner cells of which have become stored with food materials, and are protected by a corky envelope formed by modification, when the tuber is fully formed, of the cell walls of the outer cell layers. In *Anthoceros tuberosus* we may presume that the internal cellular masses, as well as the ordinary tubers, can give rise to new plants, and hence if the thallus becomes

¹ Pfeffer. Die Oelkörper der Lebermoose. Flora. Jan., 1874.

Fig. 1

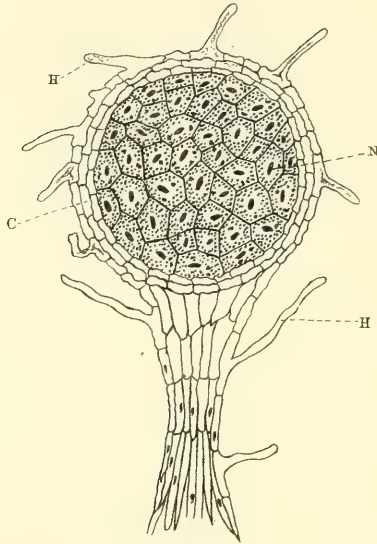
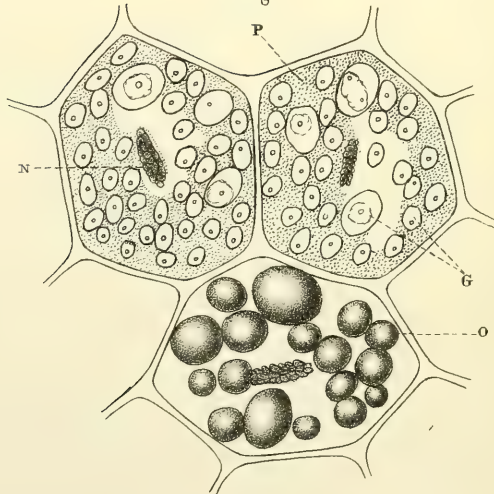


Fig. 2.



dry and dies there will still remain several living cellular masses, filled with food materials, which will be enclosed and protected by the remains of the dead thallus. These would probably be able to survive a considerable time and then give rise to new plants under circumstances favourable to their germination. It is possible that this plant forms the cellular masses in the thallus before it produces the stalked tubers, and, thus, early secures protection against extinction by drying during hot periods. That this is a possible explanation is supported by the fact that, in the dry herbarium specimens at my disposal, the histology of the cells of these internal food-laden cells is quite good, and the normal shape of the cells is retained, whereas the ordinary cells of the thallus are shrunk and collapsed.

The specimens used in this investigation were obtained from the Carrington Herbarium in the Manchester Museum, Owens College, and the work was carried on in the Botanical Laboratory of the College during the Lent Term of this year, under the direction of Professor Weiss, to whom I am indebted for advice and criticism.

EXPLANATION OF FIGURES IN PLATE III.

Fig. 1.—Longitudinal section of a tuber (with its stalk) of *Anthoceros tuberosus*, $\times 100$.

Fig. 2.—Three cells from the internal portion of the tuber, $\times 1,000$. In the two upper cells the proteid granules are shown, and in the lower one the oil drops.

C. Cork cells.
G. Proteid Granules.
H. Hairs.

N. Nucleus.
O. Oil-drops.
P. Protoplasm.

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ON RACHIOPTERIS CYLINDRICA, WILL.

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In his ninth memoir "On the Organisation of the Fossil Plants of the Coal Measures,"¹ the late Professor Williamson described a series of plant remains from the Lower Coal Measures of Halifax, under the name of *Rachiopteris cylindrica*. The genus *Rachiopteris* he had previously adopted for the reception of a number of isolated Fern petioles whose connections were unknown, and in referring the specimens to it, he only did so provisionally, as he was "far from certain" at the time that they were "true Ferns."² As to the nature of the fragments, he was undecided whether they were parts of roots or parts of stems.

The description given by Williamson in 1878 is a brief one, based apparently upon a small number of microscopic preparations, and, so far as I can discover, no further observations have been published on the subject. In the present communication I propose to give a more detailed account of the plant than was possible when Williamson wrote of it, and then to consider whether or not the knowledge since acquired throws any light upon its affinities. The specimens on which I have mainly relied are a number of sections prepared by Mr. James Binns, of Halifax, and now in the Cash Collection at the Manchester Museum, Owens College, but these have been supplemented by others.

Anatomy and Histology.

Transverse sections of *Rachiopteris cylindrica* have a circular or elliptical outline. The diameter of the circular ones varies slightly

¹Phil. Trans., 1878.

²Loc. cit. p. 350.

from an average of 2 mm. ($\frac{2}{25}$ in.), while the elliptical ones are somewhat larger, and measure for the most part 2.1 mm. ($\frac{1}{12}$ in.) by 1.9 mm. ($\frac{1}{13}$ in.). It is obvious, therefore, that the objects to be dealt with are small, but there is nothing to show that they are in an immature state. In most of them one recognises without difficulty (Fig. 1) a central cylinder or stele, surrounded by a cortex, and a peripheral or epidermal layer. The stele, when single, is circular in transverse section, with a diameter varying between 0.4 and 0.75 mm. ($\frac{1}{60}$ and $\frac{3}{100}$ in.). In many cases, however, it is preparing for, or in a state of, division, and is then more or less elliptical, measuring 1 by 0.8 mm. ($\frac{1}{25}$ by $\frac{1}{30}$ in.). The cortex, including the epidermis, varies in thickness from 0.4 to 0.8 mm. ($\frac{1}{60}$ to $\frac{1}{30}$ in.).

The Epidermis.

The peripheral layer or epidermis is not usually quite distinct, but when it is, as in No. 115,¹ it presents itself as a single layer of cells. No signs of stomata have yet been seen in it. In some sections, such as the one just referred to, it is provided with a covering of multicellular hairs, the density of which varies in different specimens, while in some no hairs are visible. In these last, however, it is not certain that the outermost layer is actually the epidermis. For the most part the hairs are seen only in transverse section. They are very rarely, and then for short lengths only, presented in longitudinal section. As in the epidermal cells, no cell contents have as yet been met with in the hairs.

Putting together the details observable in various fragments, the hairs may be described as filaments made up of a single row of cells placed end to end. At the base, what appears to be a sort of pedestal is sometimes seen, but no indications of anything of the nature of a terminal gland have been found. From the fact that transverse sections of the stem show the hairs, when present, also cut, for the most part, transversely, it seems probable that the latter were appressed rather than spreading.

¹ Here and throughout the figures refer to the Register of the "Cash" Collection of sections of Carboniferous Plants in the Manchester Museum, Owens College.

The Cortex.

The cortex is, apparently, cellular throughout, but the outer part is usually more or less differentiated from the inner. The former, or hypoderma, consists of elements which in the transverse section are polygonal, or rounded in shape, and of relatively large size. The walls show some degree of thickening, which, however, diminishes from without inwards. Longitudinal sections show the elements to be much elongated in that direction, and, in form and appearance, to be sclerenchymatous.

The inner part of the cortex is composed of cells which are somewhat smaller and rounder in transverse section than the elements of the hypoderma. Towards the stele they diminish in size, become somewhat compressed radially (as was noted by Williamson),¹ and are arranged in concentric layers. They show a certain amount of wall thickening, which increases from without inwards, and the innermost elements are elongated longitudinally. In the middle part of the cortex, where the hypoderma and the inner parenchyma run into one another, the cell walls are thinner and often much crumpled. In young specimens a complete zone of thin-walled elements occupies this region, but in older ones it is occupied by a series of radial lacunæ, separated by cellular partitions (Fig. 1). From the appearance of the tissues abutting on these lacunæ, it seems probable that their origin was lysigenous rather than schizogenous.

The contents of the cortical elements are somewhat remarkable, and present some interesting modifications. In one or two specimens the contents of both hypoderma and inner parenchyma are in the form of contracted utricles, as may be seen in the marginal section on No. 102. But in the second section on the same preparation, as well as in other cases, the utricular form is restricted to the hypoderma, and the contents of the inner parenchyma are in the form of granules, which remind us of the stored starch of recent plants. In the majority of the preparations, however, the cortical cells contain certain sharply defined black bodies, of a rounded or ellipsoidal shape, and with an even contour (Fig. 2). Frequently they are seen to be enclosed in a sort of vesicle, the cavity of which they do not fill, and whose wall is, therefore, somewhat removed from the body itself. The bodies are

¹ Loc. cit. p. 350.

small compared with the size of the elements in which they lie, and two or more are frequently seen in the same element, especially in longitudinal sections like No. 113. In the specimen figured by Williamson¹ they are very numerous, and are carefully represented, but are not referred to in the description. In most instances where the black bodies are present, the granular and utricular forms of cell contents are absent, but not in all. Thus, in No. 115 the contents of the hypodermis are utricular, while those of the inner parenchyma are represented by the peculiar black bodies. In No. 106 we have both the black bodies and the granular contents, but the distribution of each is irregular.

The nature and origin of these peculiar black bodies are points not easily determined. The first question that arises is whether they are actually portions of the cell contents or adventitious bodies that have found their way into the plant from without. Against the latter view must be set the fact that they are absent from the tissues of other plant fragments, and found in all preparations of *Rachiopteris cylindrica* which have been fossilised simultaneously and under the same conditions. Moreover, an examination of numerous sections of other species of *Rachiopteris* found in the same situations has so far failed to show their presence as regularly and as copiously as in the species under consideration. In some sections of the roots of *Psaronius* black bodies are occasionally met with which might be compared with them; but they lack the uniformity of shape and the definiteness of contour of those found in *Rachiopteris cylindrica*. On the other hand, their frequency in this species is remarkable. Leaving out doubtful cases where fossilisation has caused the disorganisation or disappearance of the cell contents, we have in the "Cash" Collection 17 preparations of the plant which show cell contents. Of these only three fail to show the black bodies, viz. : Nos. 102, 103 and 104, and they are all cut from the same specimen. It follows that out of 15 different specimens, we have only one in which these bodies do not occur. Lastly, there are reasons for regarding this specimen as younger than the rest, and it may be that the contents of the cortical cell have not assumed their final form. It is not desirable to place too much weight on these points, but taking the whole of the facts together, they seem strong enough to warrant the

¹ Loc. cit. Plate XXIV., Fig. 80.

provisional conclusion that the bodies in question are really constituents, or derivatives, of the normal cell contents and not alien immigrants from without. On this view their mode of origin will have to be sought in the changes brought about in the process of fossilisation, but with regard to this I am not in a position to say anything.

Finally, before leaving the subject, it may be worthy of notice that the general occurrence and peculiarities of these bodies have made it possible to use them to some extent as a diagnostic character of *Rachiopteris cylindrica*, and with such good results that determinations first made by their aid have been subsequently confirmed by more rigorous methods.

Endodermis.

At the innermost part of the cortex, where it abuts on the central cylinder, one naturally expects to find an endodermis, and the sections have been carefully scrutinised for indications of its presence. The result is not so completely successful as could have been wished, since it still leaves some doubt whether a specially differentiated endodermis is or is not always present. The case appears to be somewhat similar to that of *Lycopodium clavatum*, for we find here also thick-walled elements abutting on the stele, and here a well-marked endodermis cannot always be clearly recognised. But in favourable sections, *e.g.*, Nos. 104, 105 and 107, a layer of thin-walled elements is found on the inside of the thick-walled inner parenchyma, which, in the shape of its cells, their mode of union, and the appearance of the radial walls, bears some resemblance to an endodermis (Fig. 1). Its cells are larger than, and alternate with, those of the next layer on the cortical side; and they also alternate with those of the next layer within. Hence it may be regarded as the innermost layer of the cortex, or the phloeoterma of Strasburger.¹

The Central Cylinder or Stele.

If the layer of cells just referred to be really the phloeoterma, then all the tissues within it must be those which constitute the stele. On this view we can distinguish, more or less readily according to the state of preservation of the specimens, (i.) a pericycle, (ii.) phloem, and (iii.) xylem.

¹Histologische Beiträge, III.

The pericycle is seldom sharply defined, but when it is, it consists for the most part of a single layer of thin-walled cells, as large as those of the endodermis, but more variable in size and less regular in shape and arrangement. The cell contents have altogether disappeared or are too vague for determination.

The phloem is composed of thin-walled, empty, and irregularly-shaped elements of different sizes, in which little differentiation has so far been detected. It forms a complete zone round the xylem, but the breadth of the zone is not always uniform. The reference of this zone to the phloem is based more upon its topographical position than upon its structure, but in one preparation, No. 104 (Fig. 1), larger elements are embedded in it, which in form, position, and arrangement resemble the sieve-tubes seen in transverse sections of recent Ferns.

The xylem occupies the centre of the stele, and, as was pointed out by Williamson, the larger elements are usually at the periphery, while the smaller are in the centre (Figs. 1 and 2). In Williamson's figure¹ the larger and smaller elements are well differentiated, and this is not an unusual state of affairs, though in some sections the difference is less sharply marked (Fig. 1). In the majority of the transverse sections I have seen, the central elements include one or more groups of small ones, which resemble in appearance the protoxylems of recent vascular bundles. When two such groups are met with, the appearance is as if a single group had, in some way, been divided. When three, four, or five groups are met with, as is often the case, they are arranged symmetrically round the centre, and look as though they had originated by division from a smaller number.

As to the nature of the elements of the xylem, the sections at my disposal do not enable me to speak altogether without reservation. The larger are probably tracheides, as good longitudinal sections, No. 127 for instance, show. In this section the wall markings are scalariform, the pits stretching for the most part from one angle to another. But in some slightly oblique transverse sections, represented by No. 114, the pits appear to be much less elongated and approach an elliptical form.

The case of the smaller elements is not quite so certain. In the longitudinal section just referred to, they present themselves as

¹Phil. Trans. 1878. Plate XXIV., Fig. 80.

scalariform structures quite similar to the larger ones, save for the smaller diameter. The same may be said of the oblique transverse sections, where the markings of the large and small elements appear to be the same. In No. 127, however, there are suggestions at one or two points of a spiral marking, but whether these are actually spiral, or are really scalariform markings altered in some way, it is impossible to say.

The position then as regards the xylem is this. In tranverse sections we have one or more groups of small elements that may be interpreted as groups of protoxylem, but this interpretation has not so far been confirmed by satisfactory evidence that they have spiral or annular markings.

Neither in transverse nor longitudinal sections have any cellular elements been met with in the xylem, so that the xylem may be said to be wholly vascular, so far as observation has at present gone.

Division of the Stele.

The description of the stele given above does not apply to all the preparations that have been examined. In the majority a condition is met with which does not appear to have presented itself to Williamson at the time he dealt with this plant, and which shows the stele in a state of division (Figs. 2, 3, 4, 5). As this appears to be associated with the mode of branching of the plant, and the formation of lateral members, it deserves to be described with some detail.

So far as has yet been seen, the division of the stele takes place in one of two ways, being either (1) an equal division, or (2) an unequal division.

In equal division, the stele divides along a diameter in such a way that the two halves have, from the first, the same size, form, and appearance, and when the process is completed we get two distinct steles of the type already described. An early stage of the process is well shown in No. 110, where we have two semi-circular masses of xylem, inclosed in a common zone of phloem, and separated by a narrow band of thin-walled parenchyma. This parenchyma cuts through the xylem in such a way as to have the small groups of elements, presumed to be protoxylem, abutting directly upon it. As the two moieties of the stele become more and more divergent, a centrifugal development of xylem would seem to take place on the inner side of these semi-circular

masses until the circular contour is restored in each, and we have the appearance seen in No. 105 (Fig. 2). Here we have two normal strands of xylem, separated by a band of phloem, and enclosed in a zone of the same tissue. At a later stage, shown in No. 107, the two steles are found to be completely formed, and are isolated from one another by the intercalation of cortical tissue.

In this mode of stelar division we obviously have a true dichotomy of the same, and it can hardly be doubted that the process is associated with a dichotomy of the axis itself. If this inference be correct, it will follow that whatever be the nature of that axis, be it stem, petiole, or other structure, it is characterised by a dichotomous mode of branching.

In unequal division the stele divides into two portions, which from the first, are conspicuously different from one another. Ultimately they become converted into perfect steles; but they are not alike, one being of the normal type, and the other differing in important particulars. An early stage of this mode of division is met with in No. 103 (Fig. 3), where a segment of the xylem, whose height is not more than one-third of the diameter of the whole, is cut off from the rest by a narrow band of delicate parenchyma, resembling that met with in equal division. The dividing line passes through some of the smaller elements which have been referred to as probably protoxylem. The smaller segment of xylem is composed mainly of large tracheides, with only a few smaller ones on the side turned towards the other segment. As the process advances, the larger segment appears to receive an accession of centrifugally-developed xylem on the inner side, by which the detached segment is replaced, and the normal, circular form and appearance is restored. The smaller segment seems to develop little or no xylem on its inner side, and the typical form and appearance is not restored.

Thus, in Nos. 101 and 102 (Figs. 5 and 4), where we find two complete steles quite separated from one another, which have arisen by unequal division, it is clear at a glance that the two strands of xylem are very different from one another. The normal stele needs no description. The other presents a xylem, semi-lunar in form, with small elements on the flattened side and much larger ones on the convex side. The number of preparations of this type of stele is not large, and their phloem is not clear enough to justify a definite statement; but two or three of them have raised the suspicion that the phloem is mainly, if not entirely, restricted to

the convex side of the xylem. It is somewhat tantalising that the preparations should fail at this important point, because, as will be seen below, the nature of the member to which this stele belongs depends, at least in part, upon the symmetry of the stele. It is important, therefore, to decide whether the latter is radially or bilaterally symmetrical.

Lastly, in No. 115, we have two distinct and complete structures, lying near to one another, whose steles correspond respectively to those found in the same axis in No. 101.

In No. 105 (Fig. 2), in addition to the two steles already described, a third structure is found in the cortex, which is obviously some organ which, originating at or near the bifurcation, is on its way from the central cylinder to the surface. Coming off obliquely, its section is an oblique one, but in it we can easily distinguish both a central cylinder and a cortex. The cortical cells seem to have had thin walls and copious cytoplasmic contents, as if full development had not yet been attained. The central cylinder is not at all well defined, but I suspect it carried a diarch xylem strand. The real nature of this organ is not quite certain, but its endogenous origin leads me to think it is a root. Moreover, in several preparations, Nos. 102 and 103, for example, sections of the principal axis are accompanied by sections of structures that are almost certainly roots, and have some resemblance to the organ in question.

Division of the Axis.

Looking at the whole series of sections with dividing steles, it seems scarcely open to doubt that while in equal division we have an indication of dichotomous branching of the axis, in which the two members are strictly homologous with each other and their common podium, in unequal division of the stele we have an indication of the formation of some lateral organ which is not homologous with the axis from which it arises.

As to the morphological nature of this lateral organ or appendage, the evidence to hand is not sufficient to justify any definite conclusion. The suggestion that it is a foliar organ naturally and readily occurs, and that may be its character. It would be in favour of this view if the suspicion expressed above that the stele is not radially symmetrical could be converted into certainty, and this view is supported by the

negative evidence that besides the appendages in question, there is nothing else that can be regarded as suggestive of leaves ; indeed the absence of anything like an ordinary leaf-trace bundle, both in the cortex and at the periphery of the xylem, is one of the peculiarities of this plant. But of positive evidence, as just stated, there is not nearly enough to justify a conclusion.

On the other hand, the large size of the detached portion, relatively to that of the whole stele, is hardly in accordance with the foliar hypothesis. In several of his Memoirs¹ Williamson describes an unequal division of the stele of *Lepidodendron*, which in some respects resembles that met with in our plant. But in these cases it would seem that the detached smaller segment soon becomes changed into a radially symmetrical stele, similar, in essential points, to that from which it originates, a condition of things which has not been found in *Rachiopteris cylindrica*. According to Williamson, this mode of branching in *Lepidodendron* is associated with the formation of fruit-spikes or strobili, into the axes of which the branches of the stele, successively formed by unequal division, are distributed. While there is a possibility, then, that in our plant the lateral appendage may be some form of fruit or an organ axial in its nature, the character of its stele is rather opposed to such an interpretation than in favour of it.

Fig. 6, which is taken from No. 102, shows what are probably the relations in space between the axis and its offshoots. At A and B we have two normal axes which have apparently arisen by the dichotomy of a common podium. Just below A is a section, *a*, of what appears to be a root, while another, *r*, is seen just above B. Below B, at *s*, is one of the unknown lateral appendages. Symmetry of arrangement would suggest a lateral appendage above A, but the periphery of the latter is at the extreme edge of the preparation, and it is impossible to say whether such an appendage was or was not originally present. The stele of B is undergoing unequal division in a plane at right angles to that which contains all the other sections.

What is Rachiopteris cylindrica ?

Whatever interest or importance may attach to the anatomical details set forth in the preceding pages, it must be admitted that they

¹See Part II. Phil. Trans., 1872 ; Part XI. Phil. Trans., 1881 ; Part XII. Phil. Trans., 1883 ; Part XVI. Phil. Trans., 1889 ; and Part XIX. Phil. Trans., 1893.

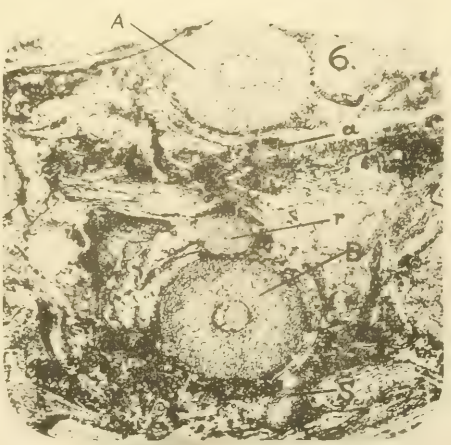
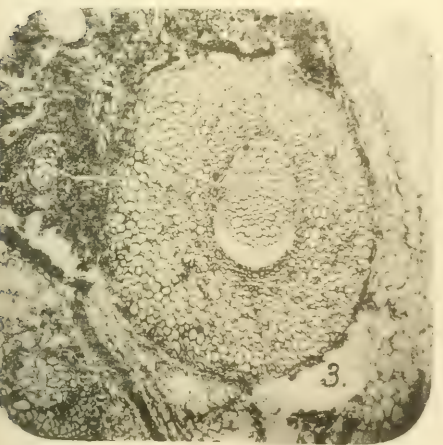
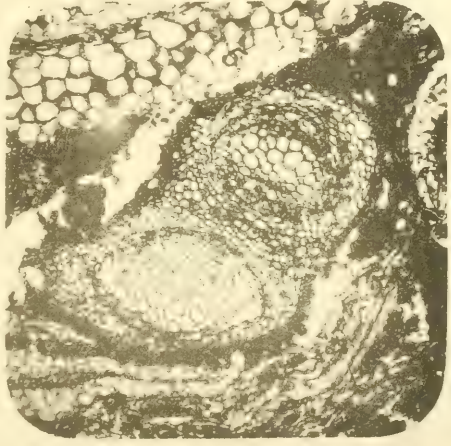
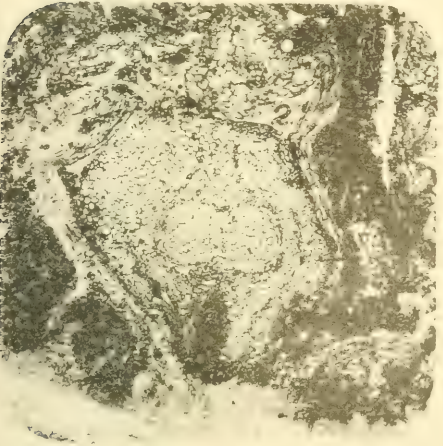
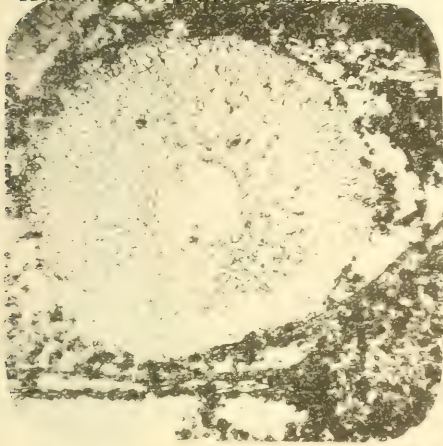
help us but little towards a knowledge of the position which *Rachiopteris cylindrica* should occupy in the Vegetable Kingdom. In the Memoir referred to at the outset, Williamson found it extremely difficult to form a reasonable conjecture on this point, and ultimately remarks, "it may be a Fern Stem, though I know no recent type of Fern which it resembles; it may be the root of some type of Fern, an idea suggested by the tendency to a concentric arrangement of the cortical cells; or it may belong to some dwarf type of Lycopodiaceous plants." Whether in the last sentence Williamson meant that it might be the root or the stem is not certain.

From what has been said of the histology of the stele, botanists will allow that its characters do not support the view that the axis of *Rachiopteris cylindrica* is a root. Nor is it otherwise with the mode of branching. We may conclude then with some confidence that it is either a stem structure—a caulome, in fact—of some kind, or the phyllopodium of a foliar organ.

The further question as to whether it should be referred to the *Lycopodiaceæ*, or to the *Filices*, cannot be answered definitely. Williamson tells us that "the entire series of [his] sections of this plant displays a considerable resemblance" to "sections of the aerial and subterranean stems of *Psilotum triquetrum*," but those I have examined hardly confirm this. Indeed, if the small elements *within* the strand of xylem are, as I presume, protoxylem elements, that fact of itself would be evidence against *Lycopodiaceous* affinities. On the other hand, it would not be inconsistent with what we know of the xylem strands of Ferns. If, therefore, our choice is to be restricted to the *Lycopodiaceæ* and *Filices*, the latter seem entitled to the preference. As, however, there are other types of Carboniferous plants in addition to those mentioned, it will be well to leave this point for future investigation.

EXPLANATION OF FIGURES ON PLATE IV.

- Fig. 1. Transverse section of *Rachiopteris*, showing undivided stele. This photograph is taken from slide No. 104 of the Cash Collection in the Manchester Museum.
- Fig. 2. Transverse section, showing division of stele into two equal parts (Cash Coll., No. 105).
- Fig. 3. Transverse section, showing unequal division of stele (Cash Coll., No. 103).
- Fig. 4. Transverse section taken a little higher up than section 3, showing beginning of separation of the two unequal steles (Cash Coll., No. 102).
- Fig. 5. Transverse section, showing completion of division of the stele (Cash Coll., No. 101).
- Fig. 6. Photograph of a larger portion of slide No. 102, than in Fig. 4 showing two stems, A and B, with their offshoots; *a* and *r* are probably lateral roots; and *s* is a lateral structure of unknown nature.
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S.B.Bolas & Co Collotype

RACHIOPTERIS CYLINDRICA.



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CONTRIBUTION TO OUR KNOWLEDGE OF THE MARINE
FAUNA OF THE FALKLAND ISLANDS.

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The work in connection with this paper has been done in the Zoological Laboratories of the Owens College, Manchester, under the kind supervision of Professor Hickson.

I must thank Dr. Harmer, of Cambridge, for his great kindness in placing at my disposal his collection of Bryozoa, and for his kind aid in identifying certain species.

My thanks are also due to Mr. Kirkpatrick for assisting me in the examination of the "Busk" Collection of Bryozoa, at the British Museum.

The material at my disposal was collected by Miss Blake, at Hill Cove, West Island, Falklands, during the months of September and October, 1896, and the specimens may be regarded as forming a typical common shore collection of that region, the shore at Hill Cove being sandy with small rocks.

Through the kindness of Mr. Standen, I have also had access to a collection of Mollusca, on some of which grew various Bryozoa, made by Miss Cobb at Lively Islands, Falklands. These were also shore forms.

In the Collection were the following species of Bryozoa :—

CHEILOSTOMATA.

I. *Beania magellanica* MacGillivray

= *Diachoris magellanica* Busk,

Brit. Mus. Cat., I., p. 54.

- II. *Beania costata* MacGillivray
= *Diachoris costata* Busk,
Challenger, Vol. X., *Polyzoa*, p. 60.
- III. *Cellaria malvinensis* Busk,
= *Salicornaria malvinensis* Busk,
Challenger, Vol. X., *Polyzoa*, p. 91.
- IV. *Cellepora pustulata* Busk,
Challenger Vol. X., *Polyzoa*, p. 200.
- V. *Cellepora pumicosa* Busk, var. *eatonensis* Busk,
Challenger, Vol. X., *Polyzoa*, p. 201.
- VI. *Cribrilina labiosa* Busk
= *Lepralia labiosa* Busk,
Brit. Mus. Cat. II., p. 82 ;
Challenger, Vol. X., *Polyzoa*, p. 133.
- VII. *Cribrilina monoceros* Busk,
Challenger, Vol. X., *Polyzoa*, p. 133 ;
Hincks, *Ann. Mag. Nat. Hist.*, (5) VIII., p. 57.
- VIII. *Lepralia adpressa* Busk, *Brit. Mus. Cat.* II., p. 82 ;
Hincks, *Brit. Mar. Polyzoa*, p. 307.
- IX. *Membranipora membranacea* Linn.
Hincks, *Brit. Mar. Polyzoa*, p. 140.
- X. *Micropora uncifera* Busk,
Challenger, Vol. X., *Polyzoa*, p. 71.
- XI. *Microporella ciliata* Pallas.
Hincks, *Brit. Mar. Polyzoa*, p. 206.
- XII. *Microporella malusii* Audouin.
Hincks, *Brit. Mar. Polyzoa*, p. 211.
- XIII. *Mucronella tricuspis* Hincks,
Ann. Mag. Nat. Hist., (5) VIII., p. 66.
- XIV. *Schizoporella hyalina* Linn.
Hincks, *Brit. Mar. Polyzoa*, p. 271.
- XV. *Schizoporella hyalina* (variety).
- XVI. *Smittia landsborovii* Johnston.
Hincks, *Brit. Mar. Polyzoa*, p. 341.
- XVII. *Porella tridentata*, sp. nov.

CTENOSTOMATA are only represented by some badly preserved fragments of the genus *Bowerbankia*, the species of which I have been unable to identify.

Of the preceding species, two are cosmopolitan in shallow water and are also found in some regions in deep water ; this fact is referred to later.

I. *Microporella ciliata*, on weed, among debris, and on *Mytilus*.

II. *Schizoporella hyalina*, on weed and shell (*Photinula*).

It is noteworthy that both these forms occur on weed.

The following species are common to the northern hemisphere, including Britain, and the Falklands :—

I. *Lepralia adpressa*, on shells (*Photinula violacea* and *Trophon muriciformis*).

Habitat : Britain (Torbay, Guernsey, Hastings). Mediterranean (Algiers, Naples, Bay of Gibraltar). Australia. Chiloe. Falklands. Mazatlan.

Moderate to deep water. Fossil—Italian pliocene.

II. *Membranipora membranacea*.

Habitat : Britain ; universal and abundant, Hvidingsoe. Høugesund (Norway). Roscoff. Finisterre (France). Adriatic. New Zealand. Australia.

Range in time—coralline crag. Palæolithic.

Occurs only in temperate seas and shallow water.

III. *Microporella malusii*.

Habitat : Britain (widely distributed and abundant). Gull-maren. Bahusia, 10-20 fath. Bergen. Finmark (Norway). Greenland. Mediterranean. Adriatic. France (S.W.). Black Sea. South Patagonia, 48 fath. Tierra del Fuego. Falklands. Valparaiso. New Zealand.

Fossil—coralline crag, on *Terebratula*. Older pliocene (Castrocaro).

The following occur in north and south temperate seas, but not in Britain, nor the tropics :—

I. *Beania magellanica*, growing on an Ascidian (*Molgula gregaria*).

Habitat : Adriatic. Australia, 2-10 fath. New Zealand. Kerguelen. Cape Horn. Falkland Islands.

It appears to occur only in shallow water.

II. *Cellepora pustulata*, on *Patella venosa*.

Habitat : Island of Capri (Italy). Victoria (Australia). New Zealand. Marion Island.

The specimen, though fairly large, is much water-worn.

It is interesting to note that the only known northern habitat of these two species is the Mediterranean.

The following species is the only one which occurs in north and south temperate and cold seas, *and in the tropics* (Florida).

Smittia landsborovii, on shell (*Trophon muriciformis*).

Habitat: Britain. Florida. Greenland. South Africa.
Falklands. Australia. Arctic Seas. Davis Strait.

Fossil—var. *crystallina*—Scottish glacial deposits.

The following species occur only in the southern hemisphere :—

I. *Beania costata*, on weed, in shallow water.

Habitat: Australia. Kerguelen. Cape Horn. Falklands.

II. *Cellaria malvinensis*, erect, in fairly shallow water.

Habitat: Petane (New Zealand). Strait of Magellan. 45 fath. South Patagonia. Victoria (Australia). Kerguelen. Marion Island. New Hebrides (S. Pacific), 70 fath. Cape Horn. Falklands. Fossil in tertiary of New Zealand.

III. *Cellepora pumicosa*, var. *eatonensis*, among debris, and encrusting shell.

Habitat: Kerguelen, 28 fath. and 45-127 fath. W. of S. America, 45° 31' S., 78° 9' W. Falklands.

IV. *Micropora uncifera*, on weed.

Habitat: Mid South Atlantic. Tristan D'Acunha. Nightingale Island, Inaccessible Island. Cape Horn.

V. *Cribrilina labiosa*, on shells (*Mytilus magellanicus* and *Terebratula*).

Habitat: Falkland. Simon's Bay (Cape of Good Hope).

VI. *Cribrilina monoceros*, on *Mytilus edulis*.

Recorded from :—

Mid N. Pacific, 3,125 fath. Australia, 35 fath. New Zealand. Marion Island. Strait of Magellan, 175 fath. Between Strait of Magellan and Falklands. Bass Strait. Cape Horn. Falklands, 12 fath.

Fossil: tertiary deposits. Bairnside, Victoria (Australia). Napier and Petane (New Zealand).

VII. *Mucronella tricuspis*, on shell (*Mytilus unguatus*).

Habitat: Australia, 38 fath. Simon's Bay (Cape of Good Hope). Prince Edward Island. Tierra del Fuego. Chiloe. Falklands, 5-12 fath. S. America.

VIII. *Porella tridentata*, sp. nov. On shell (*Euthria antarctica*) Falklands.

Of the foregoing list of species, the following have not, I think, been hitherto recorded from the Falklands :—

1. *Cellepora pustulata*.
2. *Lepralia adpressa*.
3. *Membranipora membranacea*.
4. *Smittia landsborovii*.
5. *Micropora uncifera*.
6. *Microporella ciliata*. The variety *personata* was recorded by Darwin from the Falklands, but not the true species.

Of 16 species of Bryozoa in this collection, eight have been found only in the southern hemisphere. Five have been found in the north and south temperate regions. One occurs in the north and south temperate regions and in the tropics, and two are cosmopolitan.

Notes on the Species of Bryozoa in this collection.

The zoecia of *Microporella ciliata* seem larger than those of the British specimens. In structure I think they more closely resemble those of the Californian specimens.

Lepralia adpressa var. Busk. The surface of the zoecium is strongly grooved, as described by Busk of the species occurring at Chiloe (see Busk, *Brit. Mus. Cat.*, Vol. II., p. 82) but there are, in addition, certain large pores which occur round the margin of each zoecium at the base of each triangular furrow (see Figs. 1 and 2). These pores I have also seen in Busk's "Chiloe" specimen at the British Museum, but they are neither so numerous nor so well marked as in my specimen.

Avicularia (Fig. 3) of two kinds occur, which have not hitherto been described; one appears to be the ordinary beak-like form, but is often slightly irregular in shape (Fig. 3, *a* and *b*); the other is circular in outline, with a spatulate mandible (Fig. 3, *c* and *d*). The avicularia are very irregularly distributed over a colony; sometimes five or six neighbouring zoecia possess one or even two, whilst not one of the remaining zoecia of the colony bear any.

In one or two cases, knobbed cells are seen (Fig. 1, *a*), which are characteristic of the British species (see Hincks, *Brit. Mar. Polyzoa*, p. 307). I have seen no trace of an ovicell.

Porella tridentata, sp. nov.

Zooecia hexagonal, separated by fairly deep linear furrows; surface convex and punctured by large irregular pores which, in some cases, are definitely arranged round the margin.

Secondary orifice horse-shoe shaped or inversely subtriangular, with a lateral raised collar meeting in a sudden depression behind (Fig. 4, *b*), often a sinus in front, containing a small avicularium with a rounded mandible (Figs. 4 and 5, *b*). In many cases a spatulate avicularium is present to the right of the secondary orifice (Figs. 4 and 5, *a*).

Deep down in the orifice can be seen a large median denticle with two lateral ones (Figs. 4 and 5, *c* and *d*); because of this feature it has been thought fit to call the species "*tridentata*."

The ovicell (Fig. 5, *Ov.*) is semicircular in outline, convex in front, somewhat granular, with one or two groups of irregular punctures.

Zoarium encrusting shell (*Photinula violacea*) and of a dirty pink colour.

Porella tridentata is somewhat like *P. concinna* (Hincks, *Brit. Mar. Polyzoa*, p. 323). It differs from the latter in having two lateral denticles in addition to the median one which is present in *P. concinna*. It is also somewhat larger, and the pores are bigger and irregular in shape. The spatulate avicularium appears to be constant in position, while the general shape of the secondary orifice seems to be somewhat different.

P. tridentata differs from Jullien's *P. malouinensis* (see *Cap Horn Expéd.*, p. 57) in that the pores are larger and fewer in number. *P. malouinensis* appears to have no spatulate avicularium or denticles, and the secondary orifice is somewhat different. The ovicell agrees with Jullien's description of that in *P. malouinensis*, which, however, he does not figure.

A consideration of the geographical distribution of the Bryozoa in this collection from the Falkland Islands, is of special interest at the present time because of the controversy about the origin of the north and south extra-tropical marine faunas.

Murray¹ is of opinion that "if there were once a nearly universal climate over the whole of the ocean, then it is possible that there was

¹ Murray "On the Deep and Shallow-water Marine Fauna of the Kerguelen Region of the Great Southern Ocean." (*Trans. R. Soc. Ed.*, Vol. 38 (1896), p. 343; also *Challenger Summary of Results*).

a universal littoral marine fauna." When cooling set in at the Poles, then the animals with pelagic larvæ would be killed out, or be forced to migrate towards the warmer tropics. By limiting their reproductive process to the summer season, some of the organisms with free swimming larvæ would live on in the temperate regions. With the disappearance of the shallow-water fauna from the polar regions, its place would be occupied by organisms from the deeper mud line, few of which have pelagic larvæ. In this way the similarity and, in some cases, identity between the polar faunas, and the likeness of many shallow-water polar animals to deep-sea species, might be explained.

The cooling of the waters at the Poles would cause vast migrations of forms towards the warmer seas, where metabolic changes would be greater; this would cause the struggle for existence to be intensely severe in the tropics, and would result in a rapid formation of species, while many would become extinct. On the other hand, the metabolism being less in the temperate and colder waters, and the struggle for existence being less severe here than in the warmer waters, there would be less tendency for the species to become modified, and many would remain true; hence the similarity between the North and South temperate faunas.

Ortmann,¹ whilst acknowledging the possibility of the existence at one time of a universal fauna, contends that the cooling at the Poles did not arrest the capability of variation, but that the bipolar forms now existing must have passed through a greater range of variation than the tropical forms; in other words, that the tropical fauna has remained more or less true, while the temperate and bipolar forms are derivatives of ancestral forms.

He admits that a form with a well-developed adaptative faculty may have passed through all the varying conditions of temperature, etc., without becoming extinct. The changes due to climatic conditions being similar at both Poles, two faunas resulted from the primitive material, one Arctic, the other Antarctic.

He also holds that the likeness between the north and south polar faunas is in many cases a *secondary reappearance*, and is dependent on the adaptative capability of the inhabitants of the Poles. He does not think that identical species can result in both polar seas *from a*

¹ Ortmann "Ueber 'Bipolarität' in der Verbreitung mariner Thiere." *Zool. Jahrb. (Abth. f. Syst.) Bd. 9* (1896), p. 571.

common descent. He maintains that an exchange of both polar forms can take place *through the deep sea*, on the ground that, among Crustacea, the Cosmopolitan genus *Pontophilus* shows a decided tendency to retire into deep water, but only occurs in the tropics in deep water. He suggests that many forms which have been recorded from northern and southern seas, but not from the tropics, may occur in the tropics *in deep water* and have consequently escaped capture.

Ortmann further maintains that the migration of forms may take place from the northern hemisphere through the tropics, to the southern hemisphere along the west coast of America and Africa, because of the comparative low temperature in tropical regions along these coasts. This is confirmed in the Decapods, and the reverse—*i.e.*, the migration of forms from the southern to the northern hemisphere—in the case of the Isopod *Serolis*.

Before discussing the bearings of these two theories, it would be useful to consider the distribution of the genera in the collection.

The genera represented are :—

CHEILOSTOMATA.

Beania, *Cellaria*, *Cellepora*, *Cribrilina*, *Lepralia*, *Membranipora*, *Micropora*, *Microporella*, *Mucronella*, *Schizoporella*, *Smittia*, *Porella*; and, among the CTENOSTOMATA, *Bowerbankia*.

All the species of *Beania*, with one exception (*B. hirtissima*), occur north and south of the tropics in temperate regions, but not within the tropics. *B. hirtissima* has been recorded from Cape Verde Islands, which lie within the tropics. All the species, except the British *B. mirabilis*, occur in shallow water.

The genus *Cellaria* is cosmopolitan. It occurs in deep and shallow water in the temperate zone. The depths at which it occurs in the tropics I have not been able to ascertain. It occurs in the fossil tertiary strata.

Cellepora. The *Challenger* obtained 30 or 31 species of this genus, of which the North Atlantic yielded three, from depths varying from 51-400 fath.

The South Atlantic yielded 9 species, 5-600 fath.

„ Kerguelen region „	6	„	20-500	„
„ Australian „ „	12	„	2-40	„

(One species, an aberrant form, doubtfully referred to this genus, was found in 2,600 fath.).

The North Pacific region, 4 species, 10-30 fath.

„ South „ „ 2 „ „ one from 45 fath., the other from 1,325 fath.

The genus is cosmopolitan, and appears to belong to shallow water, yet evidence shows that it has a wide bathymetrical range.

Cribrilina. This genus inhabits north and south temperate regions, but only one species (*C. floridana*) has been recorded from the tropics (Gulf of Florida). The genus is fossil, occurring in the French cretaceous, Austro-Hungarian miocene (coral and red crag), Italian pliocene, boulder clay (Wick).

The species *C. monoceros* is notable in that it occurs in very shallow as well as in very deep water. Off the west coast of the extreme south of South America it has been found at a depth of 1,325 fath., in the North Pacific at a depth of 3,125 fath., Strait of Magellan 25 fath., Tierra del Fuego and Patagonia 19 fath., Cape Horn 40 fath., Falklands 4-12 fath. My specimens were picked up on the beach. The facts of its occurring in the tertiary deposits, its presence in the north and south temperate regions, and its absence from the tropics, tend to support Murray's argument, according to which *Cribrilina* may be looked upon as a true representative of a primitive, universal, marine, littoral fauna.

On the other hand—and this is supported by the fact that this species does occur in very deep water elsewhere—it may be that this species exists in the tropics at great depths, and has thus escaped capture.

Lepralia. This genus occurs in the north and south temperate zones, and within the tropics; all the deep-sea forms occur in the temperate regions; the forms living in shallow water occur in the tropics as well as in the temperate regions. This is rather interesting, for it shows that the tropics do not form an insuperable barrier for all species, between the two temperate zones. Then, again, according to Ortmann's view, one would expect to find the deep-sea forms nearer the Equator, if the deep sea affords a passage between the two temperate zones.

The species *L. adpressa* occurs north and south of, but not within the tropics, in shallow and moderately-deep water. It occurs fossil

in Italian pliocene, Austrian miocene, and tertiary formations at Reggio (Italy). The distribution of this species gives evidence in support of Murray's view.

Membranipora. The genus is cosmopolitan, chiefly in shallow water, but it also occurs in deep water.

M. albida, Tongatabu (Pacific), 21°S., 18-20 fath. Bermuda, 38° 37'N., 450 fath. Singapore.

M. crassimarginata, Bass Strait, 38-85 fath. Heard Island, 75 fath. Tristan D'Acunha, 110-150 fath. Gulf of Florida, 13-60 fath.

M. multifida, Cape of Good Hope, 450 fath. Challenger station 320, 37° 17'S., 600 fath., green mud.

It is notable that the species occurring at great depths are found only in temperate regions. The *tropical* forms occur in *fairly shallow* water.

Membranipora membranacea occurs in north and south temperate zones, but not within the tropics.

Micropora. Genus extends back at least to the chalk period. It occurs in north and south temperate zones, as well as the tropics, in shallow to fairly deep water (greatest depth recorded, 150 fathoms). The species *M. uncifera* is recorded only from the southern hemisphere.

Microporella. Genus cosmopolitan.

Microporella ciliata is also cosmopolitan; the specimens taken at greatest depths have been limited to temperate regions, namely: Bahusia, on the Falmouth and Lisbon cable, 47° N., 89-205 fath.; and the coast of Norway, 300 fath. The tropical specimens occur in fairly shallow water.

The species *M. malusii* occurs north and south of, but not within, the tropics in fairly shallow water (10-50 fath.). It occurs fossil; coralline crag, older pliocene (Castrocaro).

Mucronella. The genus is cosmopolitan, from fairly deep water, but the species *M. tricuspis* appears to be restricted to the southern hemisphere, from shallow to fairly deep water, 12-150 fath. Fossil—tertiary—New Zealand. The species occurring at the greatest depths occur also in temperate regions, with one exception—Challenger Station 122, off East coast of South America, 9° 5' S.; the species *M. castanea* occurs from 32-100 fath., and, with this exception, all other tropical species occur in fairly shallow water. Many of the species of this genus are fossil, occurring in coralline crag, middle pliocene, upper pliocene, palæolithic, Scottish glacial deposits, &c.

Schizoporella. The genus is cosmopolitan. The species *S. hyalina* is cosmopolitan, it occurs on shells, stones, weed, etc., from shallow to deep water, it is fossil, and occurs in coralline crag, Scottish glacial deposits, post-pliocene deposits (Canada). Greatest depth: of species 100 fath. (Davis St.), of the genus 300 fath. (off Norway).

Both the cosmopolitan species *Schizoporella hyalina* and *Microporella ciliata* occur fossil, and might be remnants of a once universal fauna. Evidence shows that these forms have been able to withstand all changes of temperature and altered conditions of life, without either becoming extinct or undergoing modification so far as the hard parts are concerned.

Smittia. The genus appears to be cosmopolitan. It is found among the fossil tertiary deposits. It inhabits shallow and moderately deep water, the greatest recorded depth being 600 fath. (*S. smittiana*).

Smittia landsborovii appears to be characteristic of north and south temperate and cold seas, from shallow water to great depths. Fossil: Scottish glacial deposits.

The species *S. trispinosa* occurs in temperate and tropical zones, in shallow water and at great depths.

Porella. The genus is cosmopolitan, and is represented in the tertiary deposits. It occurs in shallow water chiefly, but does also occur at moderate depths.

These results, as far as the *Bryozoa* are concerned, seem to support Murray's theory on geographical distribution.

Each genus represented in the collection occurs fossil, and also occurs in the north and south temperate zones, as well as in the tropics; in fact, most of the genera are cosmopolitan.

Many of the *species* are represented in the *tertiary deposits*. This shows that the changes of climate and altered conditions of life, have not affected their "tertiary" structure; as many of these forms occur only in the two temperate zones, there is reason to believe that they have retained their common ancestral structure.

The fact of many of the species occurring in the deep sea hardly supports Ortmann's theory, for many of them occur at very great depths only in the temperate regions; in the *tropics* they occur in *shallow* water. Their presence in the deep sea is, I think, the result of accident.

ANTHOMEDUSÆ.

MARGELIDÆ.

Hippocrene macloviana Haeckel, *Das System der Medusen*, p. 99.

Peculiar to Falklands. Soledad Bay (Lesson). Stanley Harbour.

The genus (after allowing for Haeckel's weeding out of synonyms) is curious in its distribution, in that the species *H. macloviana* is the only representative in southern seas, and even this has, as yet, only been recorded from the Falkland Islands. The other members of this genus are found in the temperate and cold regions of the northern hemisphere as well as in the north tropical zone.

PORIFERA.

In the collection are two species of the genus *Sycon* :—

Sycon ciliatum Fleming. *Habitat*: Europe. New to Falklands.

Sycon ramsayi Lendenf. *Habitat*: Australia. New to Falklands.

One small specimen.

The genus is cosmopolitan in shallow to moderately deep water.

POLYCHÆTA.

NEREIDIFORMIA.

I. *Nereis caroni* M'Intosh, *Challenger*, Vol. XII., p. 223.

Habitat: East of South America. Fernando Noronha, 25 fath. Marion Island, 69 fath. Kerguelen, 20 fath. Falklands, 5—10 fath.

II. *Nereis patagonica* M'Intosh, *Challenger*, Vol. XII., p. 228.

Habitat: East of Strait of Magellan. New to Falklands.

III. *Nereis kerguelensis* Baird?, *Challenger*, Vol. XII., p. 225.

Habitat: Kerguelen. New to Falklands.

IV. *Nereis atlantica* M'Intosh, *Challenger*, Vol. XII., p. 219.

Habitat: Cape Verde Islands. New to Falklands.

The genus is widely distributed in north and south temperate and tropical seas, from very shallow to very deep water (1,520 fath).

The Polychæte species represented in the collection from the Falkland Islands appear to be peculiar to the southern temperate zone, although most of the genera are widely distributed in the north and south temperate and cold seas, as well as in the tropics.

V. *Lagisca magellanica* McIntosh, *Challenger*, Vol. XII., p. 82.

Habitat: Strait of Magellan, 175 fath. Kerguelen, 127 fath.

The genus appears to belong to the southern hemisphere, being widely distributed in that region, and in the tropics. It occurs also in the northern hemisphere, but is rare.

There were also present in the collection some fragmentary specimens belonging to the genera *Terebella* and *Cirratulus*, but they were too badly preserved for identification.

GEPHYREA.

Phascolosoma capsiforme Baird, *Proc. Zool. Soc.*, 1868, p. 83;

Selenka's *Sipunculiden*, p. 27.

Numerous specimens of this species were found on roots of basket kelp after storms.

This species is peculiar to the Falkland Islands. The genus is cosmopolitan in shallow to very deep water.

MOLLUSCA.

Out of 45 species of Mollusca from Lively Island, Falklands, which Mr. Standen¹ has identified, 4 occur in the tropics as well as in the southern hemisphere; one ranges through the southern hemisphere, the tropics and the northern hemisphere, *Crepidula dilatata*, which extends all along the west coast of America from Patagonia to Alaska, and also occurs in Kamtschatka; 40 are found only in the southern hemisphere, 29 of which occur only in South America and the Strait of Magellan, whilst 5 are peculiar to the Falklands.

ECHINOIDEA.

Goniocidaris canaliculata Agassiz, *Revision of Echini*, p. 395. A single, young, somewhat damaged specimen.

This species has an extensive distribution. Southern oceans, 1,600-1,975 fath. Sandwich and Navigator Islands. Natal. Falklands, 5-12 fath.

It ranges along the southern extremities of all the southern continents and extends north of the equator to Japan.

¹Melville, J. C., and Standen, R., "Notes on a Collection of Marine Shells from Lively Island, Falklands" (*Journ. Conchol.*, IX., 4).

G. canaliculata has a wider distribution than any other species of this genus, which is restricted, with this exception, to the southern hemisphere and to the tropics.

An interesting fact concerning this species is that it extends through the tropics to the northern hemisphere along the western shores of the Pacific, and not along the *eastern* shores, as one would expect. This is still more interesting when we note that this species occurs at the southern extremities of America and Africa.

HOLOTHUROIDEA.

Cucumaria mendax Théel, *Challenger*, Vol. XIV., *Holothuroidea*, p. 65. The specimens are young and under average size. The species is restricted to the Falklands. The genus is cosmopolitan.

ASTEROIDEA.

- I. *Asterias cunninghami* Perrier, *Arch. Zool. Expér.*, t. IV., p. 339.

Habitat: Falklands and Strait of Magellan. Peculiar to this region.

The genus is cosmopolitan, from shallow water to 1,250 fath.

- II. *Porania magellanica* Studer, *Challenger*, Vol. XXX., p. 363.

Young specimen. *Habitat*: W. of Patagonia. Peculiar to the southern portion of South America.

The genus is widely distributed in north and south temperate and tropical seas, from 15 to 6,000 fath.

OPHIUROIDEA.

- I. *Ophiothrix magnifica* Lyman, *Challenger*, Vol. V., *Ophiuroidea*, pp. 215, 216. *Proc. Boston Soc. Nat. Hist.*, Vol. VII., 1860, p. 254. *Habitat*: Coast of Chili. Not previously recorded from Falklands. Peculiar to South America.

The genus is cosmopolitan, from very shallow to fairly deep water.

- II. *Ophiomyxia vivipara* Studer, *Monatsb. K. Akad. Berlin*, 1876, p. 462; *Challenger*, Vol. V., *Ophiuroidea*, p. 245. *Habitat*: Cape of Good Hope, 150 fath. Kerguelen. S. W. of South America. Strait of Magellan, 55-70 fath. Between Magellan and Falklands. Has not been recorded from the Falklands before.

Of the 4 species of this genus known :—

- I. *O. vivipara* is only found in the southern hemisphere.
- II. *O. australis* occurs in South Australia and south temperate region as well as the tropics.
- III. *O. flaccida* occurs off Bahia and off Bermudahs, *i.e.*, in south tropical and north temperate zone.
- IV. *O. pentagona* occurs only in the northern hemisphere.

From the preceding one may conclude that, while the genus is widely distributed in temperate and tropical regions, the species, though overlapping each other to a certain extent, are somewhat limited in their distribution.

Of 6 representatives of the Echinoderms in the collection, 3 species are peculiar to South America, 2 of which are found in the Strait of Magellan, as well as the Falklands ; one is peculiar to the Falkland Islands. Two species are apparently distributed over the southern hemisphere, one of them extending beyond the Equator to the north temperate region.

BRACHYURA.

a) CATOMETOPA.

PINNOTHERIDÆ.

Halicarcinus planatus White, *Ann. Mag. Nat. Hist.*, Vol. XVIII, 1846, p. 178, is widely distributed over the Antarctic region, and is said to be the only Brachyurous Decapod proper to that wide area of distribution (Stebbing, *Crustacea*).

(b) CYCLOMETOPA.

CANCRINEA.

CANCRIDÆ.

Xantho crenatus Milne Edwards, *Crustacea* Vol. I., p. 396. Coasts of Peru. New to Falklands.

MACRURA.

ANOMURA.

(a) LITHODEA.

LITHODIDÆ.

Paralomis verrucosus Dana, *U.S. Expl. Exped.*, XIII., *Crust.*, Pt. 1, p. 428. Falklands. Common in E. portion of Strait of Magellan, not further W. than C.

Negro. Genus taken south and north of tropics, but not within tropics.

(b) PAGURODEA.

PAGURIDÆ.

Eupagurus comptus White. Peculiar to Falklands, and Fuegian region.

ISOPODA.

IDOTEIDÆ.

Edotia tuberculata Guérin-Méneville, *Iconographie du Règne Animal de G. Cuvier T. III. Crust.*, p. 34. *Habitat*: Confined to Strait of Magellan and the Falklands.

SPHÆROMIDÆ.

Sphæroma gigas Leach, *Dict. Sci. Nat.* t. 12, p. 346; Milne-Edwards, *Crustacea* Vol. III., p. 205. *Habitat*: Strait of Magellan. Falklands. Australia. New Zealand. Kerguelen. Aucklands (Southern Hemisphere).

AMPHIPODA.

Orchestia chilensis Milne-Edwards, *Crustacea*, Vol. III., p. 18. *Habitat*: Mediterranean and coasts of Chili; not previously recorded from Falklands.

Of the seven species of Crustacea in this collection of common shore fauna, one is common to the northern and southern hemispheres (*Orchestia chilensis*), two are distributed over the temperate portion of the southern hemisphere, and four are peculiar to the neighbourhood of the Falklands.

Paralomis. The genus occurs north and south of the tropics but not within the tropics; of 3 species, 2 occur in moderately deep to deep water, 310-600 fath.; the third, *P. verrucosus*, appears to be a shallow-water form.

Halicarcinus. The genus appears to be widely and universally distributed over the southern portions of the three great continents in the southern hemisphere.

Xantho. Genus cosmopolitan, and fossil.

Eupagurus. The genus is distributed in north and south temperate

regions as well as the tropics, but the species of this genus appear to be very limited in their distribution. The depths vary from 0 to 700 fathoms.

Edotia. The distribution of this genus appears to be somewhat doubtful. A species, *E. bicuspidata*, occurs in the Arctic seas. I have been unable to ascertain if the genus is represented in the tropics.

Sphæroma. The genus appears to be almost universally distributed over the temperate and tropical areas, but the species appear to have a very limited distribution.

Orchestia. The genus appears to be cosmopolitan in temperate and tropical littoral waters; the species of this genus, like those of other genera in this collection, are limited in their distribution.

Regarding the seven genera represented in this collection: three (*Eupagurus*, *Sphæroma*, and *Orchestia*) are widely distributed in temperate and tropical waters; one (*Xantho*) is cosmopolitan; one (*Paralomis*) has been recorded from the north and south temperate regions, but not from the tropics. One (*Halicarcinus*) is confined to the southern hemisphere: and the distribution of one (*Edotia*) is doubtful.

The distribution of the genus *Paralomis* in northern and southern temperate seas, but not in the tropics, cannot be said to support Murray's view, for I do not think this genus has been recorded as occurring fossil. The tendency of this genus to retire into deep water might be said to support Ortmann's view, but there is not much evidence to turn the balance in favour of either one or the other.

There appears to be no evidence among the representatives of Crustacea in this collection of a passage from one temperate zone to the other, along the west coasts of America or Africa.

TUNICATA.

ASCIDIE SIMPLICES.

Boltenia legumén Lesson, *Centurie Zoologique*, 1830, p. 149;
Challenger, Vol. VI., *Tunicata*, p. 88. *Habitat*: Falk-
lands, and southern extremity of South America.

The genus appears to be specially characteristic of north and south temperate seas, but has not, I think, been recorded from the tropics.

Molgula gregaria Lesson = *Cynthia gregaria*, *Cent. Zoolog.*, p. 157; *Challenger*, Vol. VI., *Tunicata*, p. 73. *Habitat*: Limited to Strait of Magellan and the Falkland Islands. It appears to have been found only in shallow water.

The genus appears to be almost universally distributed over the temperate portion of the southern hemisphere.

Comparison of the common shore fauna of the Falkland Islands with that of Britain.

It is interesting to note that there is a certain resemblance between these two faunas, but it is more clearly marked in some groups than in others. This may be due, to a certain extent, to the great or small number of species of the groups represented in the collection.

Of the 16 species of Bryozoa represented, 6 (of which two are cosmopolitan) are also found on our shores.

Of species belonging to other groups, one (*Sycon ciliatum*) is British.

All the genera (13) of Bryozoa in the collection are represented in the British fauna; of these, 8 are cosmopolitan, the remainder are found only in temperate and tropical waters.

Of the 22 genera belonging to other groups, 15 are British, 2 are restricted to the southern hemisphere, 4 are found in the southern hemisphere, tropics, and northern hemisphere (Japan); the distribution of one (*Edotia*) is doubtful.

Of the 24 species, exclusive of the Bryozoa, occurring in this collection, 19 have been found in the southern hemisphere only; of these, 7 are more or less uniformly distributed over the temperate portion, and 12 (three of which are peculiar to the Falkland Islands) have been recorded from and about the southern portion of South America. Three have been recorded from north and south temperate regions only; one from north and south temperate regions and the tropics; one from tropics and southern hemisphere only.

The evidence gained from a study of the distribution of the common shore fauna of the Falkland Islands, points to a near and close relationship, among the majority of forms, between the faunas of the temperate portions of the three great continents, including the islands in temperate latitudes of the southern hemisphere.

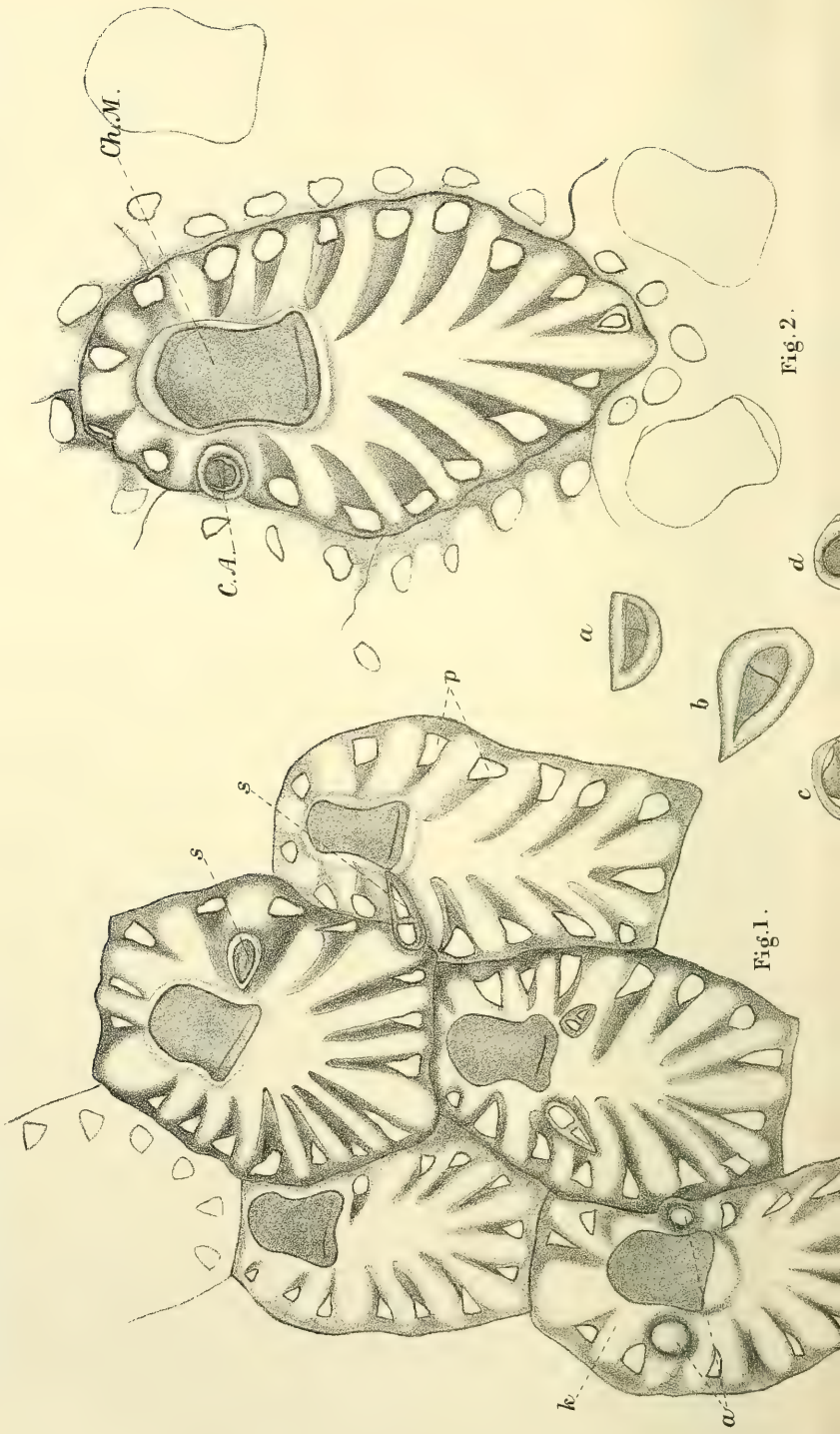
Distribution of species, exclusive of Bryozoa, in the Collection.

	N. & S. temperate.	N. & S. temp. + Tropics.	Temperate. Southern Hemisphere.	Temperate. South America.	Falklands.	Tropics and Southern Hemisphere.
Cœlent. Tera.					<i>Hippocrene macloriana</i>	
Porif.	<i>Sycon ciliata</i>		<i>Sycon ramsayi</i>			
Vermes.			<i>Nereis eatoni</i> " <i>kerguelensis</i> <i>Lagisca magellanica</i>	<i>Nereis patagonica</i>		<i>Nereis atlantica</i>
Gephy- rea. Poly- chaeta.					<i>Phascolosoma capsiformis</i>	
Echinoderm.		<i>Goniocidaris canaliculata</i>	<i>Ophiomyria vivipara</i>	<i>Asterias cunninghami</i> <i>Porania magellanica</i> <i>Ophiothrix magnifica</i>	<i>Cucunaria mendax</i>	
Crustacea.	<i>Orchestia chilensis</i>		<i>Halicarcinus planatus</i> <i>Sphaeroma gigas</i>	<i>Xantho crenatus</i> <i>Paralomis verrucosus</i> <i>Eupagurus comptus</i> <i>Edotia tuberculata</i>		
Tuni- cata.			<i>Boltonia legumen</i>	<i>Molgula gregaria</i>		
Total 24.	2	1	8	9	3	1

EXPLANATION OF PLATE 5.

- Fig. 1. *Lepralia adpressa*, var. *Busk*. Group of zoecia, magnified about 260 diam.
k, knobbed cell.
a, knobs. Characteristic of British species.
s, spatulate avicularium.
p, pores round margin between furrows.
- Fig. 2. Single cell, magnified about 380 diam.
C. A., circular avicularium.
Ch.m., chitinous mandible.
- Fig. 3. Avicularia, magnified about 380 diam.
a and b are avicularia of the ordinary beak-like type.
c and d are circular avicularia, showing mandible in two different positions.
- Fig. 4. *Porella tridentata*. Portion of colony showing disposition of zoecia, magnified about 260 diam.
a, spatulate avicularium,
b, lateral raised ollar, meeting behind in a depression.
c, median denticle.
d, lateral denticles.
RA, median avicularium with rounded mandible.
- Fig. 5. Single cell, magnified about 380 diam.
a, spatulate avicularium.
b, median avicularium with rounded mandible.
c, median denticle.
d, two lateral denticles.
Or, or cell.





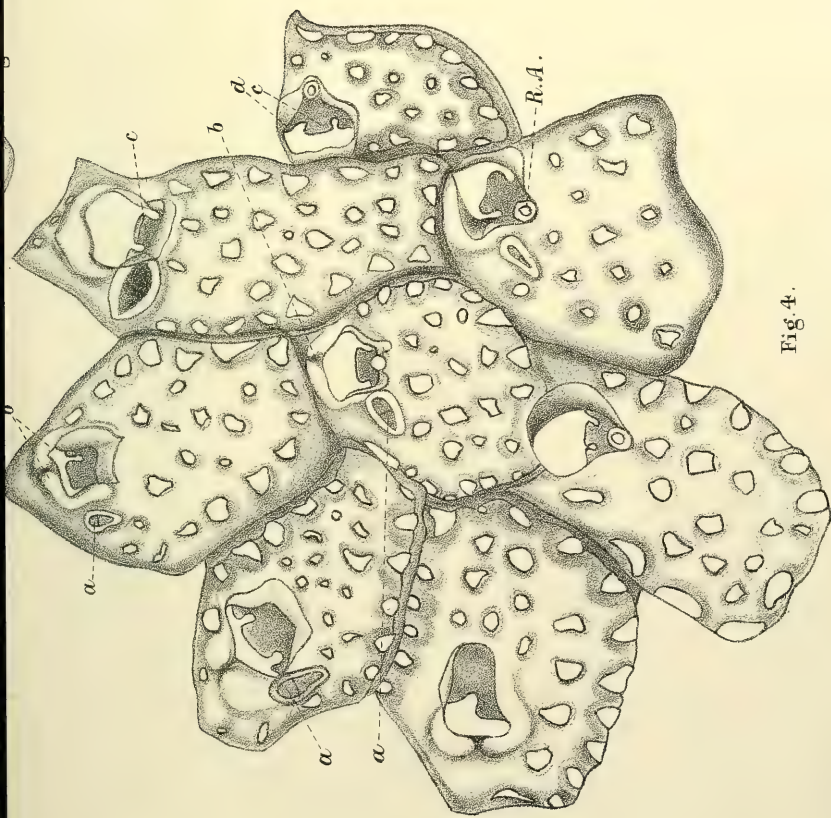


Fig. 4.

E.M. Pratt del.

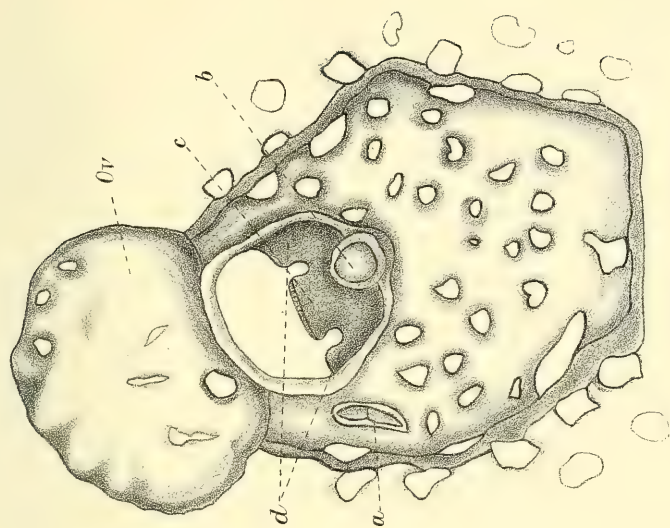


Fig. 5.

Mintern Bros. lith.

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THE HABITS AND STRUCTURE OF ARENICOLA MARINA.

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With Plates VI.—X.

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I.—DISTRIBUTION: VARIETIES: HABITS.

The common lugworm and its coiled castings of sand are familiar objects on almost all the sandy and muddy shores of Western Europe, but the exact geographical range of the species is doubtful. It has been recorded from the shores of North Siberia, Spitzbergen, Iceland, and Greenland (Wirén, 1883; Levinsen, 1883). On the north-east coast of America it has been found from the Bay of Fundy to Long Island (Verrill, 1881). On both sides of the Atlantic, latitude 40° N. marks approximately the southern limit of *Arenicola marina*. South of this it is replaced in the Mediterranean by *A. Ulaparèdii*, Lev., and

by *A. cristata*, Stimps., the latter also ranging on the west side of the Atlantic from Cape May (N.J.) to the Caribbean Sea. Its reputed occurrence on the north coast of Alaska (Murdoch¹), at Vancouver Island (Marenzeller, 1887), Coquimbo, and South Africa requires confirmation.

An abundant, widely ranging, and undoubtedly old form such as *Arenicola*, might be expected to vary considerably in its habits and structure, though it has not hitherto been ascertained how far this is the case. Having paid special attention to this point, we have found that there are (at least on the Lancashire coast) two varieties of *A. marina*, differing in habits, structure, and times of maturity, and that there is, in addition, considerable individual variability.

(1) From high-water mark down to the beginning of the Laminarian zone, the common shore lugworms (or "lugs," as fishermen call them, in contradistinction to the second variety, or "worms") sink their U-shaped burrows to a depth of from one to two feet below the surface. One end of the burrow is marked by a casting, the other by a "countersunk" hole, through which the head of the lugworm is protruded when the tide comes in. The size and colour of the animal vary with the amount of muddy organic matter in the sand. Where there is comparatively little mud, the *Arenicola* average about seven inches in length and are somewhat transparent, so that the superficial blood-vessels can be clearly seen through the thin body-wall. The gills, which are not very strongly developed, are composed of nine to eleven branches, each provided with three to five pairs of short lateral twigs (Pl. VI., Fig. 3). The proboscis and prostomium are only slightly pigmented, and being very vascular, appear red in colour.

Where, however, the amount of organic matter is considerable, the worms are usually about ten inches long, and their prostomium, proboscis, gills, and epidermis are black. The gills are better developed than those of worms living in purer sand. These differences are probably due to more abundant nutrition. The time of maturity of both these forms of the littoral variety on the Lancashire coast is the summer, while at St. Andrews they are found mature from February to September.

(2) The second variety occurs on the Lancashire coast at the upper

¹ 'Proc. U.S. Nat. Museum,' Washington, vol. vii., 1884, p. 522.

part of the Laminarian zone. Almost all the *Arenicola* from this zone (which can accordingly be obtained only at low spring tides) are of this kind, which when fully mature, as it is from February to May, is probably one of the largest Polychæts of our shores, measuring as much as fifteen inches in length and three in girth. It is almost black, the prostomium proboscis, and the base of the gills being markedly so. The tail is shorter in proportion to the length of the body than in the littoral variety. The burrows are of considerable length, three feet or more, and are not U-shaped, but simply vertical. Like those of the littoral variety, they are lined by a greenish coating of mucus. The dark "worms" appear to keep nearer the surface of the sand in cold weather than in summer—at least, during the winter of 1893-4 large numbers were thrown up on the beach at Blackpool.

The most distinctive character, however, of this "Laminarian" variety is the gill (Pl. VI., Fig. 2), which presents a structure hitherto only known in *Arenicola cristata*, Stimps. Instead of the somewhat simple gill seen in the shore lugworms, there is in the "Laminarian" variety a highly developed pinnate structure, consisting of about twelve branches united by a connecting membrane at their bases, and bearing ten or more pinnules on each side of the main axis. Such a gill is undoubtedly a much more efficient respiratory organ than the gill of a shore lugworm, though it does not appear to possess the same power of contractility as the latter, and hence probably does not contribute so much to the movement of the blood. In some old specimens the gills lose many of their finer branches, perhaps owing to friction or to the attacks of enemies,¹ and in such cases there is an approximation to the type of gill seen in the littoral variety, though a certain amount of difference is always observable.

Thus there appear to be two varieties of the common lugworm on the Lancashire coast, distinguished by their habits, external features, and periods of maturity, but there are no important structural points of difference.

The habits of *Arenicola marina* at the breeding season are still to a large extent unknown, and developing eggs have not hitherto been obtained. It has been stated that, when mature, the animal is in the habit of swimming freely (Ehlers, 1892, *a*), but we are unable to confirm

¹ See the curious account of the ravages of *Corophium longicorne*, by d'Orbigny, 'Journal de Physique,' 1821.

this. The post-larval stage, however, appears to be, for a short time, pelagic (Benham, 1893).

The curved burrow of the shore lugworm is formed by the combined action of the proboscis, the swollen anterior region of the body, and the waves of muscular contraction which pass along the body from behind forwards. When the proboscis is everted and pressed into the sand, the prostomium is slightly retracted into the body. The proboscis is withdrawn full of sand, again everted, and the body is thrust forward, partly by contraction of the longitudinal muscles, partly by a peristaltic wave produced by the circular ones. The anterior end is in this way rendered swollen and tense, and is able to enlarge the burrow, and thus a passage is gradually eaten through the sand, smoothened by contact with the skin, and lined by the mucus secretion of the epidermis. The gill-region being narrower than that which precedes it, is thus, to a certain extent, protected from friction, while, as if to ensure this, the notopodial pencils of bristles are directed so as to protect the gills. After burrowing vertically downwards for a depth of from one to two feet, the worm forms a horizontal or oblique gallery, and then a second vertical one which ends at the "countersunk" hole, through which the anterior part of the worm may protrude, and so bathe the gills in fresh sea water.

The amount and value of the work done by lugworms has been estimated on the shore of Holy Island by Mr. Davison (1891), and has also been adverted to by Mr. Hornell under the name of "cleansing of the littoral." Mr. Davison finds that the castings are larger and more numerous above than below half-tide; and as the result of several estimates and measurements he calculates that on the Holy Island Sands, the entire layer of sand, to a depth of two feet, passes through the bodies of the lugworms which live in it, once in twenty-two months, and that in a year the average volume of sand per acre, which is brought to the surface in the form of castings, is 1,911 tons, representing, when spread out, a layer of thirteen inches in thickness over the surface of the sands.

2. EXTERNAL FEATURES.

Segmentation.—The body is divided into an anterior chaetigerous portion, a middle branchial one, and a posterior caudal region or tail. The first region begins with the prostomium, and is followed by a short

achæteous portion (Fig. 1, *MET*), which in many specimens appears to be composed of four annuli, divided, however, by secondary circular markings. The first chætigerous annulus is produced into a strongly marked ridge, just behind which the notopodial setæ (*Chn.*¹) are inserted, the corresponding neuropodia (*Nm.*¹) being very short and containing only a few setæ. The intervals between the chætigerous annuli are subdivided into rings, of which there are, in the "Laminarian" variety, 2 2 4 4 4 . . . , and in the littoral variety 2 3 4 4 4 . . . respectively.

The chætigerous annuli do not mark the true somites into which the body is divided. From a consideration of the internal anatomy (see p. 94) we have reasons for believing that, in the middle region of the body, the second groove behind each chætigerous annulus marks the boundary between the somites. A somite is, therefore, composed of a chætigerous annulus together with three annuli in front of, and one behind, it. The parapodia are not situated at the beginning, but slightly behind, the middle of the somites to which they belong, thus confirming Benham's observations on the post-larval stage (1893).

The anterior region of the body is thus composed of the prostomium, six chætigerous somites, and a region between these, made up probably of two somites, but the exact number is somewhat doubtful. (See Plate VI., Fig. 1, and explanation, p. 120.)

The second or branchial region of the body is composed of thirteen somites, and is distinguished by the presence of gills, a pair of which are attached to a slight fold of the skin just behind the notopodia. The first gill is variable, usually fairly well developed, but always smaller than the rest and sometimes absent. The gills about the middle of the branchial region are frequently, but not always, the largest. Both the gills and notopodia are very sensitive, and are retracted from time to time on the application of stimuli, such as a strong light. This contraction of the gills proceeds sometimes as a wave down the body, and as Milne Edwards (1838) pointed out in his classical paper, considerably assists the circulation of the blood. The neuropodia in the branchial region extend towards the mid-ventral line, so as almost to meet, and are only separated by a groove which marks the line of the nerve cord. This groove is continued on to the prostomium by a pair of diverging arms ("Metastomial grooves") underlying the circum-oesophageal nerve connectives (Pl. 4, Fig. 19, *C. Mt.*).

The tail, which is devoid of setæ and gills, is marked by a large number of secondary annuli, crowded together at first, but arranged in distinct somites of about five each, towards the hinder end. The caudal region varies much in length; some specimens have about thirty somites, but the number is not constant possibly owing to the tendency of the worm to throw off the last few segments when irritated.

There is no change in the internal organs to mark the somite which bears the first gill, but the transition from the branchial to the caudal region is accompanied by the loss of parapodia, oblique muscles, and branchial vessels.

External Apertures.—The mouth (Pl. IX., Fig. 19, *C. MO.*), when the proboscis is withdrawn, is a slightly crescentic transverse slit, bordered by papillæ and somewhat overhung by an upper lip. The anus, which is terminal, is often protruded, and the thin vascular swollen lips of the aperture project behind the last caudal segment.

The opening of the "nuchal organ" is a fairly wide slit on the upper and hinder border of the prostomium (Pl. IX., Fig. 19, *A* and *B*, *NV.*). Through this aperture, sea water (or a mixture of sea water and the secretion of the surrounding glandular cells) is probably introduced.

The openings of the otocysts are difficult to see. They lie behind the prostomium on each side of the anterior end in the position marked *OT.* (Pl. IX., Fig. 19, *A* and *B*). Each is placed at the point of intersection of the first transverse groove following the prostomium, with the oblique "metastomial" groove which marks the position of the nerve commissure.

The nephridial openings (Fig. 1, *NO*), six in number on each side, though not so distinct as in some species (*e.g. A. Claparèdei*), are not difficult to find. The first is placed behind at the upper edge of the fourth neuropodium, and the other five in corresponding positions on the succeeding somites. They are minute slightly oblique slits, sometimes exhibiting tumid lips.

Skin.—The skin is subdivided into raised polygonal areas separated by corresponding shallow grooves, and is noteworthy in being devoid of special glands. Wirén (1887) has shown that the grooves are composed of columnar cells containing pigment granules, the raised areas being made up partly of larger cells containing still greater quantities of pigment granules and partly of clavate mucus-forming cells, which produce the slimy covering of the animal with which the burrow is lined.

The 5 per cent. formalin solution of the epidermal pigment is fluorescent, but does not yield any absorption bands, merely cutting off the rays at the blue end of the spectrum. In successively thicker layers of this solution, first the violet, then the blue, and lastly the green portions of the spectrum were cut off.

MacMunn (1889), however, has shown that the alcoholic extracts of the integumental pigment shows a band in the blue and green (λ 503—468); that the residue of this solution if dissolved in ether or chloroform yields two bands λ 503—474, and λ 465—446; and that the residue of this solution again being dissolved in nitric acid gives two bands, λ 500—468, and λ 472—443, so that a chlorophan-like lipochrome is present. It is probable that the pigment (melanin) of the skin is derived from the lipochrome of the yellow "glandular" tissue of the stomach, since the alcoholic extract of the latter yields a similar absorption spectrum.

Further investigation will be required to show in what way the transference of the pigment from the yellow peritoneal cells to the epidermis is brought about, and whether the dark coloured, hairy-looking investment of the ventral vessel and its branches (Pl. VII., Fig. 5) contributes to the melanin of the skin. In this connection the inter-muscular extension of the coelom, bringing it almost into contact with the epidermis at certain points, must be borne in mind (see p. 29).

Setae.—The notopodial setae are long capillary structures averaging 6 mm. in length, and bearing several rows of minute free and pointed hair-like processes (Pl. VIII., Fig. 10). The neuropodia in the anterior somites, which at first contain few setae, gradually extend by addition of new ones at their ventral edge, so as to almost reach the mid-ventral line (Pl. I, Fig. 1). By isolating the entire band of the setae the different stages in their development may be seen. The youngest setae are always at the lower end of the series; the point of each seta is formed first, then the toothed ridge, and lastly the shaft. The fully-developed ventral seta is frequently almost smooth, owing to the wearing down of the teeth behind the apex. The middle of the shaft is straight, the inner end bent ventrally, and the outer end bent slightly dorsally, ending with a finger-shaped process bordered on the convex side by a toothed ridge, while on the concave side it is slightly produced at one point into a minute process (Pl. VIII., Fig. 12, *proc.*). This process is more constant in the Laminarian than in the littoral variety. It

appears to correspond, in position, to the characteristic tufts of hairs on the ventral setæ of the Maldanidæ.

According to the age of the specimen the ventral setæ differ in shape, and in the development of the toothed ridge. In setæ from a small specimen (17 mm. long) the apex was bent more sharply on the shaft than in old examples, and the teeth were very prominent (Pl. VIII., Fig. 9). Apparently the production of fresh ventral setæ goes on slowly throughout life, and the form which they assume before being cast out of the body, varies at different ages. Their size of course varies with the age of the worm to which they belong (see Pl. VIII.), but in a worm of average size their length is about .5 to .8 mm.

3. GENERAL ANATOMY OF THE INTERNAL ORGANS (Pl. VII.).

In opening the body-cavity by a dorsal incision, the middle part of the alimentary canal is usually forced out through the cut by the pressure of the somewhat viscous coelomic fluid. Normally this portion of the canal, being longer than the section of the coelom in which it lies, is swung to and fro by the movements of the body. This freedom of motion is ensured by the absence of mesenteries, by the absence of any vessels running from the body-wall into the dorsal vessel, and by the length and flexibility of the branchial and nephridial vessels, which are the only connection between the stomach and the body-wall.

The coelom is exceedingly spacious, and continuous from one end of the body to the other. In front it is divided transversely by the origins of the buccal retractors (*B. Sh.*), which form a sheath round the proboscis, and by three septa or diaphragms (Pls. VII. and VIII., Figs. 5 and 6). The first of these septa (*Dphm.*) is placed obliquely, arising below behind the level of the first neuropodium, and being inserted dorsally in front of the first notopodial sacs. The result of this arrangement is that between the first and second diaphragms two pairs of setal sacs occur, caused by the forward shifting of the upper edge of the first diaphragm (Fig. 5). The second and third are inserted both above and below, opposite the second groove behind the second and third chaetigerous annuli. Between the first and second diaphragms, dorsal and ventral mesenteries occur, supporting the corresponding vessels; and it will be noticed that the dorsal mesentery ends in front, exactly where the first diaphragm would be inserted if it corresponded with the other two. The third diaphragm is perforated by the funnels

of the first nephridia. There are, then, three diaphragms and not, as so often stated, four; and, while affording valuable evidence of the extent of the first and second chætigerous somites, they do not help in determining the number of segments which compose the achæitous portion following the prostomium.

Behind the last diaphragm the body-cavity is unsegmented up to the base of the tail. The segmental arrangement of the organs, however, can be recognised by taking the funnels of the nephridia as marking the anterior ends of the somites. The slight amount of connective tissue supporting the long afferent and efferent vessels (segmental vessels) (Pl. VII., Fig. 5) of the nephridia and gills, may be regarded as the remains of the septa. Allied species of *Arenicola* fully confirm this view.

At the level of the thirteenth pair of notopodial sacs, the segmental afferent and efferent blood-vessels, which have hitherto run nearly parallel across the coelom, diverge. At the base of the tail, the connective tissue between them increases slightly in amount, septa forming which are continued down to the end of the body (Fig. 5, *C. Sp.*).

4. MUSCULATURE.

The muscles of the body-wall are arranged in (1) an outer circular sheath, subdivided in the anterior and middle regions of the body into hoops, which cause the annulation of the skin; and (2) an inner longitudinal sheath of considerable strength and thickness divided by the nerve-cord and lines of insertion of the notopodial sacs into three parts, two ventrolateral and one dorsal (Pl. IX., Fig. 23). The inter-muscular spaces are filled by coelomic fluid, and are probably lined by a delicate peritoneum.

In the anterior region of the body there are a few circular muscle-bands which are stronger and more obvious than the rest (Fig. 5, *M. Circ.*).

The oblique muscles, which divide the coelom longitudinally into three compartments, commence behind the third diaphragm, and disappear at the base of the tail. These muscles are arranged in thin broad bands, arising at the sides of the nerve-cord, and are inserted right and left into the body-wall at the level of the notopodial sacs. They partly cover the nephridia, and in some specimens a muscle-band is attached to each nephrostome.

The musculature of the buccal mass consists of a strong sheath of fibres derived from the longitudinal layer just behind the first diaphragm. This sheath, which is loosely attached to the proboscis by slips which run through the coelomic space between the two structures (Pl. VIII. Fig. 6, *B. Sh.*), is inserted into the anterior part of the proboscis. Pressure of the coelomic fluid at this point causes eversion of the buccal mass, which is withdrawn by the contraction of its muscular sheath.

The prostomium is retracted by a small sheet of muscle which arises partly from the longitudinal layer dorsally, and partly from the muscular covering of the circumoesophageal connectives ventrally, and it is inserted into the ventral surface of the brain, and the ventral and hinder edge of the nuchal organ (Pl. VIII., Fig. 6, *Nu. Tr.*).

The parapodial muscles are modifications of the longitudinal layer. One, the retractor of each notopodium, is remarkably long, reaching to the side of the nerve-cord (Pl. VIII., Fig. 13, *Rn.*). The protractors (*Pn.*) of the notopodia are six to eight in number, three to four being placed in front of, and three to four behind, the setigerous sac. They arise from the body-wall just below the dorsal longitudinal vessel, and are inserted into the base of each sac.

The position and relations of the three anterior septa or diaphragms, of the dorsal and ventral mesenteries between the first two of these, and the presence of regularly arranged septa in the tail region, have already been noted. It may be added that a pair of outgrowths from the first diaphragm lie under the oesophagus, opening anteriorly into the coelomic space in front of the first septum. They are very vascular, and contract rhythmically every three or four seconds during life, and are doubtless of use in everting the proboscis (Pl. VII. and VIII. Figs. 5 and 6, *Dph. Ph.*).

In the caudal region the intestine is attached both above and below to the body-wall by mesenteries, in which the dorsal and ventral vessels lie.

5. ALIMENTARY CANAL (Pl. VII.).

This consists (1) of an eversible buccal mass (*Bucc. M.*), of a pinkish or greenish-brown colour, which lies in front of the first septum; (2) of an oesophagus, of a light brown colour, provided with a pair of glandular pouches behind the third diaphragm; (3) of a gastric region,

with yellow glandular walls, extending from the level of the heart to about that of the twelfth or thirteenth notopodium ; and (4) of an intestine, of a dark brown or almost black colour, folded in a concertina-like manner by the caudal septa, and opening at the terminal anus.

During life the buccal mass (or "proboscis") is constantly being everted and withdrawn, carrying sand into the œsophagus. During eversion several rows of curved, pointed, vascular papillæ (*B. Pap.*) are first extruded. These papillæ (Pl. VIII., Fig. 7) in old specimens are tipped with chitin, and recall the armature of the proboscis in certain Sipunculids (*e.g. Phascolion collare*¹). Then the more globular portion of the buccal mass, covered with minute rounded processes, is protruded. Finally, when fully everted, the buccal aperture is surrounded by a few pointed pigmented papillæ, which are continuous with the lining of the first part of the œsophagus.

The œsophagus² itself is slightly looped behind the second diaphragm. It is a thin-walled distensible tube, the first part of which is lined by non-ciliated mucus-forming cells. The middle portion is lined by a cuticle, and the posterior part by cells resembling those of the stomach in bearing cilia. The œsophageal pouches (*Oe. Gl.*) are somewhat flask-shaped, and open into the cavity of the œsophagus by a short tubular stalk. They are usually greenish in colour, but have a slight reddish tinge on account of their very large blood-supply. Their blood-vessels are connected with the lateral œsophageal and dorsal vessels. The cavity of the pouch is subdivided by twenty-five to thirty incomplete partitions, produced by infolding of the wall of the pouch, and therefore covered on each side by the epithelial lining of the pouch (Pl. IX., Fig. 22). Between the epithelial lamellæ is a blood-sinus, which is slightly enlarged at the inner end and slightly thickened at the edge of each partition. The œsophageal pouches are lined by ciliated epithelium, covered with a fairly stout cuticle, and contain glandular cells. The walls of the œsophagus are marked by longitudinal and circular muscular impressions.

The stomach, marked out by the patches of yellow tissue on its walls, extends from the level of the heart to about the twelfth notopodial setæ. As we have already stated (p. 94), the stomach is bent upon

¹ Selenka, 'Die Sipunculiden,' 1883, pl. vi., fig. 74.

² The histology of the alimentary canal has been carefully investigated by Wirén (1887, p. 31). Our results agree very closely with his.

itself and loosely attached to the body-wall. The patches of "chlorogenous" tissue are at first arranged in symmetrical oval areas right and left of the dorsal blood-vessel, while more ventrally they are placed in two or three less regular series, and are separated from one another by a network of blood-vessels.¹ About the level of the tenth setæ these yellow areas all become subequal and arranged in a spiral manner, ending at the level of the fourteenth setæ.

Stomach and Intestine.—The muscular wall of the gastric region is exceedingly thin, and composed purely of circular fibres, which appear to confer very slight powers of peristalsis upon the stomach.

The mucus lining is strongly folded, and is composed of several kinds of cells. Some of the cells in all parts of the stomach are ciliated, others are apparently digestive, and a large number appear to secrete a mucus similar to that of the œsophagus, the cells themselves being discharged into the mucus which they help to form.

Commencing about the middle of the stomach (that is between the ninth and tenth segments) is a ventral groove formed by a couple of folds of its inner and lower surface. This groove² (Pl. IX., Fig. 23, *Gv.*) is provided with specially long cilia, which produce a current of mucus from before backwards. There are other smaller grooves on the side walls of the stomach and the anterior part of the intestine, whose general direction is downwards and backwards, and which open into the median ventral groove. The direction of the current in all these is from before backwards. The ventral groove is continued back to the anus. The intestine is dark brown or nearly black in colour externally. Its mucus lining is somewhat similar to that of the stomach, but is covered by a thin cuticle, and is not ciliated.

The process of digestion in the lugworm has not been at all fully investigated, but the series of events appear to be somewhat as follows. The sand or mud is mixed with the mucus secretion of the œsophagus, and is slowly carried backwards by peristaltic contraction. At the junction of the stomach and œsophagus the secretion of the œsophageal pouches is poured upon the sand. Wirén regards the contents of these pouches as acid and digestive. In several cases we have found the

¹ This network is considered by Wirén and others to be parts of a continuous sinus. We are not convinced, however, that this is really the case, and our reasons will be found on p. 101 infra.

² This groove has only hitherto been noticed by Wirén (1887).

fluid neutral. In the stomach several changes occur. The secretion of the gastric cells proper is probably digestive, and this, together with a further amount of mucus, is mixed with the sand, and shaken together by the swing of the loose gastric loop. In this way the food, which apparently consists of the organic substances¹ in the sand is brought into contact with the digestive secretion. The ciliary action of the lateral and ventral grooves probably separates the digestive substances from the sand and carries them slowly downwards and backwards. The lining of the stomach is very thin, and the lateral and ventral grooves are in specially close contact with the blood plexus, in which the flow is, probably, slowly forwards, more rapidly in the sub-intestinal vessels. It seems probable, therefore, that the blood in the visceral plexus conveys the nutritive material to the hearts, which pump it along the ventral vessel to the various parts of the body.

The action of the chlorogenous tissue round the stomach, and particularly of that in the neighbourhood of the ventral vessel and its branches, is uncertain.

6. VASCULAR SYSTEM (Pl. VII. Fig. 5).

The blood-vascular system of *Arenicola* attains a high degree of perfection. The large size of the chief vessels, the great development of the capillary system (especially on the walls of the alimentary canal), and the mechanism for promoting the flow of the blood, are features that distinguish it.

There are two chief vessels running, one above, and the other below, the alimentary tract from end to end,—the dorsal vessel, which contracts fairly rhythmically from behind forwards; and the ventral vessel, which is feebly, if at all, contractile. The walls of the gastric and intestinal portions of the gut are enclosed in a blood-plexus, and the œsophageal region is supplied by lateral vessels. The gastric vessels are connected with the ventral vessel by a pair of “hearts” placed a short distance behind the œsophageal pouches (Fig. 5. V.). These hearts drive the blood from the gastric vessels into the ventral vessel.

The dorsal vessel (*DF*) arises near the anus, and as it runs along the

¹ Saint Joseph found in an *Arenicola* a whole *Nereis* almost digested. ‘Ann. Sci. Nat.’ series vii., t. xvii., 1894, p. 127.

intestine gives off in each somite a pair of branches which are attached to the anterior face of the caudal septa, and which run downwards and forwards to open into the ventral vessel (Pl. VII., Fig. 5). Of these there may be twenty-seven to thirty pairs. In front of the caudal region each of the last seven pairs of gills returns an efferent branch to the dorsal vessel, and between these there are three or two pairs of smaller branches which run round the alimentary canal from the ventral vessel to open into the dorsal one. From the level of the twelfth setæ to the œsophageal pouches the dorsal vessel does not receive any segmental vessels from the gills or nephridia, nor does it open directly into the heart (Fig. 5). It merely receives numerous branches from the gastric plexus. In front of the heart it receives on each side a branch from the third nephridium and the fifth setigerous sac; a branch from the œsophageal pouches; and one from the second nephridium and fourth setigerous sac. It then runs on and, piercing the third diaphragm, receives a branch running on the anterior face of the diaphragm from the first nephridium and third setigerous sac. On reaching the second diaphragm it receives a branch from the second setigerous sac, and after piercing the first diaphragm receives a branch from the muscles forming the buccal sheath. Thence the dorsal vessel breaks up into capillaries around the buccal musculature, prostomium, and otocysts. From these capillaries the ventral vessel takes its origin. It gives off a small unpaired branch running in the first diaphragm and to its pouches; a paired branch arising about midway between the first and second diaphragms to the neural vessels and second setigerous sac; a single small vessel supplying the second diaphragm and the neural vessels; an unpaired vessel to the third diaphragm, to the neural vessels in that region, and to the first nephridia; a pair of branches to the neural vessels and second nephridia; and lastly, a pair to the neural vessels and third nephridia. From this point onwards the ventral vessel supplies the setigerous sacs, body-wall, nephridia (if present), and gills, by large segmental vessels. The ventral vessel is very large and turgid in the gastric region, and is surrounded by tufts of dark brown chlorogogenous tissue, which are also found in older specimens on the vessels running to the body-wall. This chlorogogenous tissue is first seen on the ventral vessel about the level of the eighth pair of setæ. In the tail the ventral vessel ends in the obliquely placed intestinal vessels which

encircle the intestine, and which form, along with the capillaries from its median terminal portion, the commencement of the dorsal vessel.

Visceral Plexus.—Wirén (1887) maintains that the intestine and stomach are enclosed in a blood sinus, thickened along certain lines which have been called the dorsal, gastric, and subintestinal "vessels." We are, however, of the opinion that the so-called sinus is a close plexus of vessels, some of which appear to have a distinct cellular lining. The dorsal vessel is, at any rate, a perfectly distinct structure with proper walls.

The subintestinal vessels (Fig. 5, S.V.), which commence just behind the heart and run backwards, are moderately large up to the level of the thirteenth setæ, but then taper rapidly and gradually disappear. They each receive seven segmental vessels. The first of these comes from the fourth nephridium, the second from the fifth nephridium and the first gill, the third from the sixth nephridium and second gill, and the other four from the third, fourth, fifth, and sixth gills. The subintestinal vessels open through the plexus into the lateral gastric ones, and so into the heart. The flow in these vessels is probably slowly forwards.

The gastric vessels give off from the "auricle" into which they expand, a lateral œsophageal vessel (*Oe. Lat.*), which, after giving off a stout branch to the œsophageal pouches, runs forwards to the buccal mass, supplying the wall of the œsophagus, as it does so, with numerous small branches.

Neural Vessels.—These are a pair of small vessels lying one on each side of the ventral nerve-cord, and accompanying it from one end of the body to the other. They arise around the nerve-connectives from the brain from capillaries of the dorsal vessel, and receive several branches from the ventral vessel (1) midway between the first and second diaphragms (2) from the vessel running in the second diaphragm (3) from a vessel just behind the third diaphragm (4 and 5) from the vessels to the second and third nephridia. Near the middle of each somite the two neural vessels are united by cross connections, which also supply the nerve-cord (Pls. VII. and VIII, Fig. 13, N.V., N.C.V.).

Behind the third diaphragm the neural vessels supply the oblique muscles by branches which run the whole length of the bands, and are connected with the outer longitudinal parietal vessel (Fig. 13).

Vessels of the Body-wall.—This parietal system of true vessels is highly developed in *Arenicola marina*. It consists of two longitudinal vessels (1) the nephridial longitudinal vessel (Fig. 22, *N. L. V.*) running just below the level of the nephridiopores, and (2) the more important dorsal longitudinal vessel (Fig. 13, *D. L. V.*), which runs just above the level of the insertion of the notopodial setal sacs. Both arise just behind the first setæ, and increase in size as they pass backwards. The former receive vessels from the nephridia, just behind which they taper and disappear. The latter, which may be traced to the anus, and are largest in the branchial region, receive branches in each somite: (1) from the segmental vessels (2) from its fellow of the opposite side. The body-wall in the dorsal and lateral regions derives its blood-supply from the nephridial and dorsal longitudinal vessels, and in the ventral region from the neural vessels. These parietal vessels (*Par. V.*) run just within the layer of circular muscles in almost every groove between adjacent longitudinal muscle-bands of the body-wall, are chiefly longitudinal in direction, but at frequent intervals there are cross connections. Branches from these vessels ramify between the bases of the epidermal cells, and are accompanied by extensions of the cœlom.

Hearts.—The hearts are a pair of muscular bulbous swellings connecting the visceral plexus with the ventral vessel on each side. Each commences with the thin-walled expansion of the gastric vessel ("auricle," Fig. 5, *A. v.*) which, after giving off the lateral œsophageal branch, opens into the ventricle (*V.*). The cavity of the ventricle is small and broken up by a spongy mass of cells. The ventricular walls are muscular, and contract from above downwards, forcing the blood into the ventral vessel. (We have sometimes seen an apparent reversal of the heart's action.) The spongy *cardiac* body arises by ingrowths from the wall of the ventricle, chiefly in the middle and ventral regions. It gradually encroaches on the blood space, so as to reduce it considerably (Pl. X., Fig. 36, *Card. B.*) in an old specimen. The cardiac body in a young specimen (Fig. 38) is much smaller, and extends obliquely across the heart, its general direction being downwards and backwards. The cells of the cardiac body in an old specimen which we have examined are loosely arranged, so as to cause the formation of a large number of intercellular spaces, some of which are of considerable size, and which are in life filled with blood (Figs. 36—38,

B.S.). Between the cells there are numerous fibres, which are probably muscular. The cells are apparently of two kinds, which, however, merge into each other: (1) cells whose protoplasm has a very vacuolated appearance, and which contain few or no granules (*Vac. C.*); (2) cells which contain a large number of yellowish granules in the protoplasm (*G.C.*). These latter cells are possibly granular, and correspond to those found in the cardiac body of other Polychaets. The function of the cardiac body may be, as Schaeppi (1894) suggests, to prevent regurgitation of the blood from the ventral vessel into the heart when the diastole commences. The "cardiac body" of Polychaets, as hitherto described, is an unimpaired structure lying in the dorsal vessel. That of *Arenicola*, however, is paired and in no way connected with the dorsal vessel. Hence a strict homology is scarcely probable.

Blood.—As Professor Lankester was the first to point out, the blood of *Arenicola* is strongly impregnated with hæmoglobin, but there has been no thorough investigation of the constituents of the plasma. Krukenberg (1882), it is true, made some experiments which led him to believe that there were no coagulable albumens in the blood of his specimens; but, as they were in a starving condition, a fresh examination is very desirable. A large quantity of albumen is certainly present, which, when the specimens are fixed, becomes very hard and brittle.

We have seen small cells (4μ in diameter) in the blood-vessels of the nephridia, but it is doubtful if these are the blood-corpuscles which we have not been able to demonstrate.¹

General Remarks on the Circulatory System.—No other system of organs shows the true segmentation of the body of *Arenicola* so well as this. The lines of demarcation between the somites from one end of the body to the other are marked by the segmental vessels passing from the ventral to the dorsal vessel and breaking up on their way in the body-wall, nephridia, or gills. Throughout the gastric region, however, this arrangement is somewhat disguised, owing to the loss of the connection with the dorsal vessel, an alteration caused probably by the necessity for leaving this part of the alimentary canal freely moveable.

¹ Since writing this we have discovered that these small cells are the blood-corpuscles.

Wirén evidently believes that there is no capillary system except in the gills and the alimentary canal. He suggests that the assimilation of food and oxygen by the tissues is effected chiefly through the mediation of the *cœlom*, which he points out is parcelled off in the intermuscular spaces, by a channelling out of the subepidermic connective tissue, into "perihæmal canals." Though this suggestion is a valuable and correct one, we have found a very perfect system of capillaries in the skin in all parts of the body, and in the nephridia and septa the same is the case. The extension of the *cœlom* into the intermuscular and subdermal spaces has, however, all the appearance of acting as the equivalent of lymph-spaces of higher forms. The transformation of the constituents of the blood into *cœlomic* fluid takes place in all probability with especial rapidity in the neighbourhood of the dark chlorogenous processes of the ventral vessel (cf. Cuénôt, 1891).

7. THE GILLS (Pl. VI., Figs. 2—4).

The general characters of these organs have been mentioned in the introductory part of this paper, and little remains to be added.

There are thirteen pairs of gills from the seventh to the nineteenth chætigerous somites inclusive. The shape varies from the short dendritic type of the littoral form to the delicate, richly-branched gill of the Laminarian variety. The gills are hollow, being out-growths of the body-wall enclosing an extension of the *cœlom*, and what little evidence we have of their development (see Benham, 1893) points to their being independent structures, and not modified dorsal cirri.

The walls of the gills, though thin, are muscular, and there are also muscular bands stretching across the cavity of the gill (Fig. 23); and Milne Edwards has pointed out that the contraction of the gills, which often proceeds like a wave from before backwards down the sides of the body, must exert a powerful influence in propelling the blood partly into the efferent vessels, and partly to the parietal capillaries.

The ventral vessel supplies all the gills with their afferent branches. The first seven pairs return the blood to the sub-intestinal vessels, and so to the heart; while the efferent branches of the remainder open into the dorsal vessel.

8. NERVOUS SYSTEM AND SENSE-ORGANS.

This system is composed of the brain, the œsophageal connectives, the ventral nerve-cord, and the nerves arising from these. We have not been able to demonstrate a visceral nervous system.

The brain (Pl. X., Figs. 25, 26) is placed in the prostomium, of which it forms the chief part, being only separated from the epidermis by blood-vessels lying in extensions of the coelom. It is a small elongated structure, measuring .75 mm. in length in ordinary shore lugs, and 1 mm. in the large "Laminarian" variety. At its anterior end the brain is divided into two stout cornua (*A. Cr.*), separated by a cleft containing blood-vessels. About the middle of the brain the cornua unite, but only for a very short distance, a second connective-tissue partition dividing the smaller posterior cornua (*P. Cr.*), which gradually taper off and end at the hinder edge of the nuchal organ (Pl. X., Fig. 25).

Sections of the prostomium of the littoral variety of *Arenicola* (immature specimens, 4" long) exhibit a thick covering of ganglion- and glia-cells, forming the dorsal surface of the brain (Fig. 24); a central fibrous portion; and a strong ventral membrane, into which the greater part of the prostomial muscles are inserted, though a few fibres are attached in front of and between the anterior cornua (Pl. X., Fig. 25). In older specimens, and particularly in mature examples of the "Laminarian" variety, the ganglion-cells are more scattered, and in other ways the brain shows greater differentiation. The anterior cornua, for example, are not only deep and thick, but give off from their dorsal surface short stout branches, along which the ganglion-cells are scattered, and which supply the prostomium. The central fibrous part of the brain also grows out ventrally in these large examples, separating the hitherto compact layer of cells and carrying them outwards or leaving them in clumps, and not evenly arranged as in young *Arenicola*.

From the anterior cornua a large nerve arises on each side, in front of the origin of the œsophageal connectives. It passes out to the under surface of the epidermis, and supplies the papillæ on the upper surface and the sides of the mouth. The epidermis of the prostomium itself is in close contact throughout its whole length with the ganglionic covering of the processes arising from the dorsal and lateral surfaces of

the brain. The posterior cornua seem to be specially connected with the nuchal organ, against which they lie and terminate (Pl. IX., Fig. 21).

The most remarkable histological feature of the brain is the close contact between the large ganglion-cells of its upper surface and the sensory epithelium of the prostomium (Figs. 20 and 24). Racovitza (1896) has figured (Pl. X, Figs. 48 and 49) a similar condition in *Clymene*. It is only at this point that the nervous system of the adult *Arenicola marina* can be said to have an epidermal position. Elsewhere it is separated from the epidermis by the circular musculature.

The circum-oesophageal nerve-connectives arise from the large anterior cornua in the form of two thick cords, covered on their outer surfaces by ganglion-cells (Figs. 20, 21, 25, *Oe. Comm.*). From them a pair of short nerves (Fig. 26, *OT. N.*) arise supplying the otocysts, and several longer ones are distributed to the oral papillæ of the ventral region of the mouth. The line of the connectives is marked externally by the "metastomial groove" (Pl. IX. Fig. 19, *C.*), and the commencement of the ventral cord by the junction of these grooves which occurs on the ventral surface just in front of the first chætigerous annulus. The nerve-cord is protected by a delicate connective-tissue sheath, a thin sheath of circular muscle, and a thin layer of epidermis. Though nearly circular in section it is somewhat flattened from above downwards, but exhibits scarcely a trace of segmentation externally or internally. The ganglion-cells are arranged in two ventral groups, while the fibrous portion of the cord is dorsal. In the tail the ganglionic masses increase in size, and are separated from the skin by a thicker layer of circular muscle-fibres. Two "giant-fibres" are present in the branchial region, a single one only in the anterior and tail region.

From the chord a paired series of nerves is given off with great regularity, one opposite each groove separating the annuli of the somites, so that there are five nerves on each side of the body in each somite. These lie in the body-wall just beneath the circular layer of muscle, and, in some places where this layer becomes obsolete, they lie just under the epidermis. Dorsally these nerves thin out and become very difficult to trace.

Sense-organs.—There is no doubt that the prostomial lobes, the nuchal organ, and the otocysts are sense-organs; but there are, in

addition, certain other structures, such as the setæ¹ of the notopodia and some of the buccal papillæ, which on account of their position, movements, and the nerves ending in them, may be considered as probably belonging to this category.

Professor Ehlers' (1892) account of the nuchal organ and otocysts is an almost exhaustive description of these organs in *Arenicola*. We have worked over the whole subject again, however, and are able to add a few points to this important paper.

The nuchal organ belongs to the prostomium, whereas the otocysts belong to the metastomium. The prostomium and the nuchal organ are found, in varying degrees of complexity, in nearly all Polychæts; the otocysts, however, occur in few and widely separated families.

The general appearance of the prostomial lobes and the opening of the nuchal organs have already been described. Seen from the dorsal service the former consists of a small median papilla and two larger lateral prominences (Pl. IX., Fig. 19), which together correspond with the single prostomial papilla of allied forms (cf. Racovitza's figure of *Leiocephalus*, 1896, pl. v, Fig. 5). In young *Arenicola* these lobes are transparent, and therefore red from the underlying blood-vessels. In old specimens they become dark-coloured and opaque from the deposition of pigment in them. In no species of *Arenicola* have eyes been discovered, although they are known to occur on these lobes in many related genera.

The prostomial epithelium is a complex of several distinct kinds of cells,—unaltered columnar elements, fusiform sense-cells, each ending in a conical prominence, glandular cells, and apparently also "wandering cells" from the body-cavity. Underneath the epithelium is a connective tissue continuous with the supporting tissue, the neuroglia of the brain, which binds together the large ganglion-cells of the cornua of the brain. The prostomial sensory structure thus formed is very sensitive to light, but what function it subserves has not been determined with accuracy.

Nuchal Organ.—To the outer side of the lateral prostomial lobes is a depression guarded externally by a fold (just above *Nu.*, Pl. IX., Fig. 19, *B.*). These two pits form the beginning of the nuchal organ and indicate its paired origin. Further back they unite to form a

¹ Retzius has described free nerve-endings on these setæ. 'Biologiska Föreningens Förhandlingar,' Bd. iii, Hefte 4—6, 1891, p. 85.

transverse groove (bordered by the hinder edge of the prostomium), which is continued inwards as a deep pit to the hinder margin of the brain (Pl. 5, Fig. 25). From the posterior cornua of the latter the nuchal organ is innervated.

In its paired form and under the names "Wimperorgane," "Wimpergrübschen," the nuchal organ is well known in almost all families of Polychæts, and a similarly placed organ is found in Sipunculids,¹ not to mention other more distantly related groups. It is always associated with the posterior lobe of the brain, and arises as a pair of pits from the surface of the prostomium. Of its development in *Arenicola*, however, we have no evidence, but the two depressions in front of the main part of the organ, together with the paired nerve-supply, point to its double nature.

The epithelium of this deep, pigmented pit (Pl. IX., Fig. 21, *Nu.*) is composed of long columnar ciliated cells, glandular cells which secrete the mucus in which the cilia work, and slender sense-cells. It seems probable that the whole organ is olfactory in function.

Otocysts.—The otocysts of *Arenicola marina* are a pair of flask-shaped structures projecting into the body-cavity close to the outer edge of the œsophageal nerve-commissures. They open externally by a couple of apertures (Pl. IX., Figs. 19, A and B, *OT*), at that point on the "metastomial groove" where the latter is crossed by the first groove of the body following the prostomium. The body of the flask is placed at an angle with the "neck," and contains the otoliths. It is lined by non-ciliated columnar sense-cells and supporting cells, which are surrounded by the nerve-fibres and connective-tissue fibrils, figured by Ehlers (1892, pl. xii.). The neck of the otocyst is made up of a columnar epithelium covered with a thick cuticle, which gradually merges into the epidermis of the external surface, and ciliated cells only occur in its lower portion. A short nerve from the œsophageal commissure supplies the otocyst.

If the otocyst of a fresh shore lugworm be rapidly dissected out under sea water and mounted, the sand-grains will be seen to execute a most extraordinary movement. Each one is rotating slowly and jostling its fellows, so that the whole contents of the flask are in a state of commotion. The fluid in which the otoliths move is slightly viscous, and

¹ Ward, 'Bull. Mus. Harvard,' vol. xxi., 1891, p. 143.

is a secretion of the walls of the otocyst, mixed with a little sea water. The sand-grains are covered with a distinct layer of some chitinous substance soluble in boiling potash. Acids have no appreciable effect upon these grains, and under the polariscope they react as quartz does. Hence it seems clear that the otoliths of *Arenicola marina* (the other species of the genus differ most remarkably in this respect, as well as amongst themselves) are quartz grains covered by an organic film, and surrounded by a fluid which is not merely sea water.

Large specimens of the "Laminarian" variety were examined without being opened under sea water, and the otocysts were mounted by us in cœlomic fluid. No movement of the otoliths was observed even in specimens which were perfectly healthy in all respects. The otoliths sometimes filled the expanded part of the organ, and it is possible that they had no room to turn round. But it appears to us more likely that if we assume the cause of the rotation to be the diffusion caused by liquids so different as sea water, in which the preparation was first mounted, and the somewhat viscous, perhaps albuminous fluid inside the otocyst; then if we mount the otocysts in the same kind of fluid which they contain, no movement should occur; and the experiment showed that in these cases no movement did occur. The whole matter is one of very great interest, especially in view of the probable functions of such an organ as the otocyst. Ehlers has suggested that the movement is due to the cilia at the bottom of the neck of the otocyst; but the same extraordinary movements are seen in the otocyst of *A. Grubii*, which is closed and has no cilia. We quite agree with Ehlers that there are no cilia in the expanded part of the otocyst where the movement has been noticed, but we are of the opinion that the quivering motion of the otoliths is not a normal phenomenon, but is due to diffusion currents.

9. NEPHRIDIA.

There are six pairs of nephridia, belonging to somites 4 to 9. Of these the first pair seems to be unrepresented in any other species of *Arenicola*, and its variation in *A. marina* points clearly to a gradual degeneration which it appears to be undergoing at the present time. It is not only the smallest of the series, but is sometimes represented merely by a funnel or by the secretory and terminal portions. Very

rarely both the first nephridia are mere funnels, and again one may be fully developed and the other rudimentary, but they are never absolutely wanting. Their small funnels, which are of a bright pink colour, are placed on the anterior face of the third diaphragm with the long axes vertical (Pl. VII., Figs. 13 and 14). One lip (the outer) is produced into processes corresponding to the dorsal lip of the other nephridia. The secretory portion is elongated, narrow, and usually brownish in colour, and the terminal portion opens just above the fourth neuropodium (Pl. VI., Fig. 1) at a decidedly lower level than is the case in the succeeding nephridiopores.

The remaining five pairs are always in adults fully developed. They are attached to the body-wall partly by connective tissue, partly by the broad bands of oblique muscle which obscure them at first sight (Pl. VII., Fig. 5). The nephrostomes are very long, and bent upon the rest of the organ. The narrow slit-like aperture has a dorsal vascular lip bearing finger-shaped or spatulate ciliated processes, and an entire ventral one. The cilia just within the mouth of the funnel are exceedingly long, and produce a current tending to carry cœlomic fluid and corpuscles into the cavity of the organ. The middle or secreting portion is brownish (in old worms almost black), owing to the excretory granules which are formed in its cells. The terminal rosette-shaped bladder, which is slightly lighter in colour, opens by a minute slit-like aperture through the body-wall, which thins out at this point (Pls. VI. and IX., Figs 1 and 22, *NO.*).

The blood-supply to the nephridia (Pl. IX, Fig. 18) is derived from the ventral segmented vessels, which divide, one branch going to the funnel of the nephridium and the other to the body-wall. The former traverses the funnel, sending a vessel into each of the ciliated processes, and giving off numerous small branches to the lips of the funnel. After traversing the funnel the vessel runs over the secreting portions of the nephridium, supplying the genital strand in its course, and finally ramifies on the terminal portion. The blood is collected again into small vessels, which open into the dorsal longitudinal or nephridial longitudinal vessels of the body-wall, from which it is returned largely to the dorsal or subintestinal vessels, but in part passes into the parietal vessels. (See note, p. 118.)

In young specimens the funnels are naturally simpler, but have similar positions and relations, as may be seen in Figs. 16—18, which

show nephridia from worms 29.5 and 44 mm. long, in which the processes on the dorsal lip are being formed. In the post-larval stage (Benham, 1893) the nephridia have no funnels, the development of which has still to be investigated.

10. CÆLOM.

The coelom of *Arenicola* is well developed, and continuous in all its parts. Not only does it form the space between the alimentary tract and body-wall from one end of the body to the other, but it is carried along with the blood-vessels into the intermuscular spaces. Thus the blood-vessels of the prostomium, of the buccal sheath, and of the body-wall generally are accompanied by coelomic canals which very probably serve as lymphatic spaces from which nutritive matters can be absorbed by the surrounding tissue, and into which waste nitrogenous substances may be excreted.

The segmentation of the body-cavity is very faintly marked. Anteriorly three diaphragms, perforated just above the nerve-cord, are present whose position and relations are indicated on Fig. 5, and Pl. VIII, Fig. 6. The whole middle region of the body is devoid of septa, which, however, reappear on the last two somites of the branchial region, and are present throughout the tail in a complete form, though they are perforated to allow of the more thorough circulation of the coelomic fluid.

Arenicola fresh from the sand exhibits a series of peristaltic waves of the body-wall from behind forwards, which can be easily seen if the gonads are sufficiently developed to cause slight swellings, which each wave carries forwards. These waves of fluid are probably of considerable physiological value. They assist the circulation of the fluid, the coelomic cells, and the developing reproductive cells. They inflate the anterior digging part of the worm, and thus assist in burrowing. By their action the contents of the gut will tend to travel slowly backwards, the weak visceral musculature being probably insufficient by itself to cause the requisite amount of movement of the sticky sand: while in defæcation the main agent is doubtless the pressure of the coelomic fluid on the intestine, brought about by violent contractions of the body-wall.

The coelom is lined by a very thin layer of flattened cells, which

undergo remarkable changes in certain parts of the body, resulting in the formation of (1) chlorogogenous tissue, (2) ova or spermatozoa, (3) cœlomic corpuscles.

The cœlomic fluid is a mixture of sea-water and globulins, among which only paraglobulin has hitherto been detected (Krukenberg, 1882, p. 87). We find that the specific gravity of the fresh fluid (including corpuscles) varies slightly, but is on the average 1·0288.¹

On exposure to air this fluid coagulates, and a delicate fibrous network is formed, binding the corpuscles together. If carmine is injected into the cœlom, it is removed by the cœlomic corpuscles, by the cells lining the cœlom and by the nephridia, and there is no trace of carmine in the cœlom after forty-eight hours.²

Cœlomic Corpuscles.—These abundant cells occur in two chief forms, which probably pass into one another. The first varies from 8 to 20 μ in length, is amœboid, and usually contains yellow or brown granules of a very highly refractive character. The pseudopodia are often grouped at the two ends of the cell (Pl. X., Fig. 24). The longer forms of this kind of corpuscle pass into the second or spindle-shaped cells of the cœlom, which measure as much as 50 μ in length, and contain no coloured granules. These fusiform elements are most abundant, and constitute the most characteristic features of the cœlomic contents.

The *chlorogogenous tissue* of the ventral vessel and its branches in the body-wall consist of groups of cells about 20 μ in length, full of large slightly yellow or deep brown granules, which are not highly refractive. The tissue in old black worms is immensely developed, so as to completely cover the vessel by the masses of hair-like threads, each thread consisting of a small blind diverticulum of the vessel surrounded by the chlorogogenous cells.

11. REPRODUCTIVE ORGANS.

Thanks to the researches of Cosmovici (1880), Cunningham (1887), Kyle (1896), and others, the true ovaries and testes of *Arenicola marina* are now known to arise by proliferation of the peritoneal covering of an

¹ It was found to be least (1·0270) in specimens which had been kept for some time in sea water, and greatest (1·0311) in those which had been kept for thirty-six hours in moist seaweed only. The specific gravity of the sea water used was 1·0264.

² Schneider, 'Arbeit. Naturf. Gesellschaft,' St. Petersburg, Bd. xxvii, Heft 1, 1890.

extension of the blood-vessel supplying the funds of the nephridia. It is not certain that there is a corresponding gonad on the first pair of nephridia, but on each of the following five pairs the gonads are present during the breeding season. In both sexes the organ is a mass of cells, from which the ova or spermatoblasts break away at a very early stage, to ripen in the cœlom. The rachis is continuous with the posterior angle of the nephrostome, and is developed around a backwardly projecting process of the nephridial vessel which comes off segmentally from the ventral vessel (Pl. IX., Fig. 18, *G.V.*).

In large *Arenicola*, at certain seasons, the vascular process has no gonad, and it is possible, as Cuénot (1891) suggests, that a formation of the amœboid corpuscles of the cœlom takes place at this point when the animal is not breeding.

After passing through the earliest stages of their development in the genital rachis, the young reproductive cells may be found at the breeding season in all stages of development in the cœlom. The ova do not exhibit any considerable changes except in size in attaining maturity. They are nourished either directly from the cœlomic fluid, or possibly (Cuénot, 1891) by the amœboid cells acting as follicle cells, though we have seen nothing to support this view. Extrusion of a polar cell (?) has been observed by us in an ovum only about half the definitive size (Pl. X., Fig. 35, *A* and *B*). In the spherical ripe ova (which measure .16 mm. in diameter) a distinct but very thin vitelline membrane is present, and a small quantity of food-yolk in the form of very small granules in the protoplasm. The production of ova by the fertile vascular processes of the nephrostomes must be extraordinarily great, since the spacious body-cavity of a large worm is eventually filled to bursting with them by the end of February.

We have not followed the development of the spermatozoa in great detail. The youngest stage which we have found in the cœlom contained eight spermatoblasts arranged round a vesicular-looking blastophore (Pl. X., Fig. 30). Further division and elongation of the outer ends of the cells to form the tails of the spermatozoa produces the stages seen in Figs. 31 to 34. The masses of spermatids are not spherical, but disc-shaped, their thickness being only about one quarter of their long diameter. They contain a cavity, the remains of the blastophore, together with a small quantity of a slightly fibrous coagulum in the centre of the cavity. Curiously enough, perfectly ripe

males were comparatively rare in March and May of this year, when mature females were abundant. In most cases the body-cavity was full of spermatids in great bundles, as in Fig. 34. The ripe spermatozoa closely resemble those of *A. Grubii*, which have been accurately figured by Claparède.¹ They measure ·058 mm. in length, and possess a curiously shaped head, ·004 mm. in length, and an extremely long slender tail (·054 mm. long). The head (Figs. 28 and 29) is divisible into three regions,—a rounded disc-like cap (*S.*) at the anterior end, which is partially divided by a median groove; the nucleus (*N.*), which is large and oval in shape; and the “middle piece” (*M.*), which bears posteriorly a depression into which the tale is inserted. This depression is formed only at the time when the spermatozoa are fully ripe. The tail (*T.*) in the specimens which we have been able to obtain appeared to be a somewhat stiff filament, which could only be bent to a comparatively small extent.

The breeding season of the “Laminarian” variety of *Arenicola marina* lasts from February to May on the Lancashire coast. The large black “worms” which may be dug out during the great spring tides of these months are then distended with ova or spermatozoa. Males and females are not distinguished by external characters, but owing to the slight discharge of gonads from the nephridiopores consequent on the tense condition of the body, it is often possible to distinguish the sex of an example without dissection. It is at present impossible to state how long these *Arenicola* live and how many times they breed.

The ordinary littoral lugworms of the Lancashire coast and of the Isle of Man are not mature in the spring, and contain at most a few very small eggs. In the summer (August) of 1896 we found mature specimens, and we believe that this variety breeds through the summer, commencing at about the time when the deeper water form has ceased.

Relation of the Nephridia to the Reproductive System.—As is well known, the ova and spermatazoa escape by the nephridiopores, but it does not seem to have been noticed before, that in both males and females the bladders of the last five pairs of nephridia are specially enlarged (Pl. III., Fig. 15, *Bl.*), and contain mature ova or spermatozoa, so that upon irritation a simultaneous discharge through all these

¹ ‘Annélides de Naples,’ 1868, pl. xix, fig. 2, *C.*

apertures may occur. In one worm only eight inches in length the bladder of the nephridium was swollen with ova so as to measure 14 mm. in length and 6 mm. in width. During the discharge of ova from the female the eggs are caught by the slimy mucus covering of the body, and, owing to the movements of the animal, collect in strings round the body. We have not observed the formation of gelatinous capsules in which the eggs may be laid, since we have not worked at the oviposition of this species, about which nothing is at present known. At certain times of the year, chiefly in the spring, the nets used by shrimpers on the sandy coast near Lytham are almost choked by the balls of eggs, each moored by two "cables" to the sand. Whether these eggs belong to *Arenicola* remains to be seen, but their form differs from that of *Phyllodoce* found so commonly in early spring.

It has generally been assumed that the number of nephridia and gonads occurring in *Arenicola marina* is typical or fairly typical of the genus, and it is usually stated that the number of both these organs is a small one (five or six). An investigation of several other species of *Arenicola*, the results of which we hope shortly to publish in full, have shown that *A. Grubii* and *A. Claparèdii* have five pairs of nephridia, and apparently the same number of gonads, whereas *A. ecaudata* has no less than thirteen pairs of nephridia, twelve of which bear large and complicated gonads of a size and complexity which is scarcely equalled by any other Polychæt. What relations exist between *A. mariae* and the other species of the genus cannot be discussed here, but it may be stated generally that the genus exhibits greater variety in the development of several systems of organs than has been hitherto suspected, and that it is no longer possible to exemplify the characters of *Arenicola* as a genus by using their particular grade of development in *A. marina* as a type.

12. GENERAL SUMMARY.

The following is a recapitulation of the new points which we have found in *Arenicola marina*.

1. On the Lancashire coast, and probably elsewhere, two well-marked varieties of *Arenicola marina* occur, differing, as the following table shows, in general appearance, in their habits, in the structure of their gills, and periods of maturity.

Name.	Habitat.	Colour.		Gills.	Breeding Season
		Adult.	Young.		
"Shore lugs," or littoral variety, 6—8" long, exceptionally 10"	The sandy and muddy shores of bays, estuaries, and harbours, extending from high water mark to and sometimes beyond low tide level Burrow U-shaped	Greenish brown or reddish black	Semi-transparent, yellowish or brown	Moderately developed Branches with 3—5 pairs of gill-plumes	July, August
"Worms," or Laminarian variety, 8—15" in length.	The sandy shore exposed at extreme low spring tides, occasionally extending above this Burrow a vertical shaft	Black or very dark brown	Dark red, opaque	Very well developed. Branches with usually about 12 pairs of dichotomously arranged plumes	January to May.

2. The cilia lining the central or gastric region of the alimentary canal are specially arranged (1) on the sides of a ventral groove which is continued to the anus, and (2) on curved shallow grooves running downwards and backwards into the former. The current caused by the action of these cilia carries a stream of mucus and of digested food slowly backwards and away from contact with the mass of sand in the gut. As these grooves are in close connection with parts of the visceral plexus, absorption may take place from them.

While the ventral groove is morphologically equivalent to the similar structure of *Oligognathus* (described by Spengel¹), and probably to the "siphon" of Capitellids, we have seen no reason for regarding it or any other part of the alimentary canal as "respiratory" in function.

3. In the circulatory system the two hearts each contain a cardiac body. This structure is composed of masses of granula and vacuolated cells, projecting into the cavity of each ventricle. Functionally they may be regarded as glandular valves preventing the reflux of blood into the gastric sinuses. While previously unknown in *Arenicola*, the "cardiac body" has been long known in allied genera (*Ophelia*, *Trophonia*, *Chlorhæma*), but as an unpaired structure in the dorsal vessel (Schaepfi, 1894). Hence, though histologically similar, it is

¹ "Oligognathus Bonelliae," 'Mitt. Zool. Stat. Neapel,' iii., 1882.

very doubtful whether the paired structure of *Arenicola*, which has no connection with the dorsal vessel directly, is homologous with the unpaired organ of other Polychæts.

Contrary to Wirén (1896), we regard the dorsal vessel as a distinct structure, the gastric blood-system as a plexus, and we find that the nephridia and body-wall, as well as the gills, are well supplied with capillaries.

4. Both the large pinnately-branching, and the smaller dendritic, types of gill occur in *A. marina*. The usual statement that the latter type of gill characterises this species, and that the former type is characteristic of *A. cristata*, must therefore be modified.

5. The brain is divided by a narrow cleft throughout the greater part of its length. The anteria cornua supply the prostomium, the buccal papillæ, and give off the œsophageal nerve connectives. The middle region of the brain supplies the upper part of the prostomium, and the posterior cornua innervate the nuchal organ.

In young specimens the almost uniform covering of ganglion-cells of the brain is in close contact with the peculiar and complex sensory epithelium of the prostomium, but in old specimens of the "Laminarian" variety fibrous outgrowths from the dorsal and lateral surfaces of the brain scatter this ganglionated covering.

6. The nuchal organ, though apparently single, shows traces of a double origin. It is probably an olfactory organ, and is developed from the posterior region of the prostomium.

7. The otoliths consist of quartz grains surrounded by a delicate chitinoid film, as Ehlers stated. The peculiar commotion observed in otoceysts mounted in sea water was not noticed in others examined in cœlomic fluid. Hence the motion is probably a result of diffusion currents.

8. The first pair of nephridia are in process of reduction. In the others the form of the funnel at an early stage is described and figured. In adult examples the terminal portions of the nephridia act as receptacles for the ripe ova or spermatozoa.

9. The specific gravity of the cœlomic fluid varies slightly, but is on the average (including the corpuscles) 1.0288, thus being only very slightly denser than sea water (1.0264).

10. The general analogies of *Arenicola* with certain other limnivoruous Chætopods are very striking. With the Sipunculids the Arenicolidæ

agree in the chitinous spines tipping the proboscis papillæ, the buccal papillæ, the strong retractors of the "proboscis," the capacious and largely unsegmented cœlom, the general character of the musculature, the thin-walled looped alimentary canal with its ciliated ventral groove, the action of the body-wall in producing waves of cœlomic fluid auxiliary to the process of burrowing and defæcation, and lastly, the pigmented nuchal organ. If we acknowledge the many points of agreement, which have for the most part arisen independently, between these two distantly related families under similar conditions of life, the true relationship between *Arenicola* and othera genera of Polychæts can only be ascertained by exercising the greatest caution in not confusing convergent adaptational characters with true genetic resemblances.

NOTE TO PAGE 110.

The vessel printed in red on Plate VII., Fig. 5, and lettered N. Eff.⁴, is in reality a solid cord of connective tissue accompanying the afferent vessel (N. Aff.⁴) of the fourth nephridium. November 11th, 1899.

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EXPLANATION OF PLATES VI.—X.

Illustrating Mr. F. W. Gamble's and Mr. J. H. Ashworth's paper on "The Habits and Structure of *Arenicola marina*."

LIST OF REFERENCE LETTERS.

A. Cr. Anterior cornua of the brain. *An.* Anus. *Au.* "Auricle" of the heart. *Bl.* Bladder or terminal part of the nephridia. *Blph.* Blastophore of spermatoblast. *B. Pap.* Papillæ of the buccal mass. *Br.* Gills. *Br. Aff.* Branchial afferent vessels. *Br. Eff.* Branchial efferent vessels. *BR.* Brain. *B. S.* Blood spaces in the heart. *B. Sh.* Sheath of retractor muscle enclosing the buccal mass. *Bucc. M.* Buccal mass. *Card. B.* Cardiac body. *Chl. Tiss.* Chlorogenous tissue on the stomach and ventral vessel. *Chn.* Notopodial chaetæ. *C. F.* Cardiac fibres. *C. Sp.* Caudal septa. *D. L. V.* Dorsal longitudinal vessel. *D. Nph.* Dorsal lip of the nephrostome. *Dph. Ph.* Diaphragmatic pouch. *Dphm.* ¹⁻³ Diaphragms or anterior septa. *Ep.* Epidermis. *G.* Refrangent granules in coelomic cells. *Ga.* Ganglion-cells of the brain. *Gast. Lat.* Lateral gastric vessel. *Gast. V.* Gastric vessels. *G. F.* "Giant fibres." *Gl. Op.* Opening of the oesophageal glands into the oesophagus. *G. S.* Granular cells of the heart. *Gv.* Ventral groove of alimentary canal. *G. V.* Gonidial vessel. *Int. V.* Intestinal vessels. *M.* "Middle piece" of spermatozoon. *M. Circ.* Circular muscles. *Mes. D.* and *Mes. V.* Mesenteries supporting the dorsal and ventral vessels between the first and second diaphragms. *MET.* "Metastomium," or achæitous portion of the body immediately following the prostomium. *M. Long.* Longitudinal muscles. *MO.* Mouth. *M. Ob.* Oblique muscles. *M. Par.* Parapodial muscles. *M. Pr.* Retractors of the prostomium. *N.* Nucleus. *N. Aff.* Afferent vessel to the nephridia. *N. C.* Ventral nerve-cord. *N. Cap.* Nephridial capillaries. *N. Eff.* Efferent vessel from the nephridia. *NLV.* Nephridial longitudinal vessel. *Nm.* ¹⁻¹⁰ Neuropodia. *No.* ¹⁻⁶ Nephridiopores. *NPH.* ¹⁻⁶ Nephridia. *NPHM.* Nephrostomes. *NS.* Nervous elements and connective tissue round otocyst. *Nu.* Nuchal organ. *Nu. Tr.* Retractor muscle of nuchal organ. *N. V.* Neural vessels. *Oe.* Oesophagus. *Oe. Comm.* Circumoesophageal nerve-connectives. *Oe. Gl.* Oesophageal glands. *Oe. Gl. V.* Vessel of oesophageal glands. *Oe. Lat.* Lateral oesophageal vessel. *O. Ot.* External opening of otocyst. *OT.* Otocysts. *OT¹.* Neck of otocyst. *Oth.* Otolith. *OT. N.* Nerve to otocyst. *Par. V.* Parietal vessels. *P. Cr.* Posterior cornua of brain. *Pn.* Protractor of notopodium. *Pr.* Prostomial lobes. *Rn.* Retractor of notopodium. *S.* Cap of spermatozoon. *S. V.* Sub-intestinal vessels. *T.* Tail of spermatozoon. *V.* Ventricle of the heart. *Vac.* Vacuole. *Vac. C.* Vacuolated cells of the heart. *V. Nph.* Ventral lip of nephrostome. *V. V.* Ventral vessel. *I. II. III. IV. &c.* Somites beginning with the first chaetigerous.

PLATE VI.

FIG. 1.—The anterior end of a large specimen of the "Laminarian" variety seen from the left side, to show the external features, the segmentation of the body-wall in relation to the internal metamerism, the nephridal apertures, and the commencement of the branchial region. The chaetous region following the fully everted buccal mass (*Bucc. M.*) extends forwards as far as the groove indicating the insertion of the first diaphragm dorsally* (*Dphm.*¹). We have considered the first chaetigerous annulus and the annulus behind this, as composing the first chaetigerous somite (*I*), although we are fully aware that, owing to the obliquity of the first diaphragm, and the absence of landmarks in the chaetous region in front of this septum, it is somewhat hazardous to delimit this first chaetigerous somite. $\times \frac{5}{8}$.

FIG. 2.—View from the right side of two somites from the anterior part of the branchial region of a specimen of the "Laminarian" variety 7 inches long. The fourth gill is shown in detail, while the third and fifth are cut down to the base of the main branches. The large size of the spreading branches and the somewhat pinnate arrangement of the lateral twigs distinguish the gill of this variety of *A. marina* from that of the ordinary shore lugworm seen in Figs. 3 and 4. The webbing at the bases of the branches is generally much more marked in old black examples than in immature dark red specimens such as the present. $\times 14$.

FIG. 3.—Fifth gill of the right side of a shore lugworm 8 inches long, to show the features characteristic of the littoral variety of *Arenicola marina*. The branches are united by extensive connecting membranes, between which the blood-vessels of the gill are faintly visible. $\times 14$.

FIG. 4.—The first gill of the right side from the same specimen as Fig. 3. The ventral branches are apparently the last to develop, and are only just budding off the secondary leaflets. $\times 14$.

PLATE VII.

FIG. 5.—Dissection of a large "Laminarian" variety, to show the general characters of the internal anatomy (conf. pp. 9 to 10). The body-wall has been cut along the mid-dorsal line, the flaps pinned back, and the alimentary canal turned over to the left side. The special features shown are the vascular system, the nephridia, the septa, and muscles. $\times 2$.

PLATE VIII.

FIG. 6.—View of a vertical longitudinal section of *Arenicola marina* taken somewhat to the left of the middle line. The thickness of the body-wall is exaggerated. The stomach has been cut away behind the heart, to show the oblique muscles and the second nephridium. The main blood-vessels only are indicated, the object of the figure being to show the exact position of the three diaphragms (*Dphm.*¹⁻³), of the buccal or proboscidal sheath (*B.Sh.*), and the relation of these to the external segmentation. $\times 3$.

FIG. 7.—Chitinoid spines covering the buccal papillae of that part of the proboscis which is first protruded during eversion. They may be compared with the figures of "hooks" from the proboscis of Sipunculids (*e.g.* Phascolion) shown in Selenka, 'Die Sipunculiden.' Caustic potash preparation. $\times 50$.

FIG. 8.—Papillæ *in situ* on the base of the proboscis of young worm. $\times 6$.

FIG. 9.—A group of neuropodial setæ from a very young *Arenicola marina* 16 mm. long. The shape and strongly-toothed ridge distinguish these setæ from those of the adult (Figs. 11 and 12). The youngest setæ are on the left side of the figure. $\times 300$.

FIG. 10.—Notopodial seta 6 mm. long. $\times 16$.

FIG. 10A.—The tip magnified. $\times 50$.

FIG. 10B.—The toothing on the notopodial seta highly magnified. $\times 450$.

FIG. 11.—Neuropodial seta ($\times 20$), and enlarged ($\times 120$).

FIG. 12.—A group of developing neuropodial setæ *in situ* in the neuropodium (*Nm.*) of a "Laminarian" specimen. $\times 70$. *Proc.* is referred to on p. 9.

FIG. 13.—The fourth and fifth chaetigerous segments of the left side of a large mature "Laminarian" specimen. The first two nephridia are shown. The figure is a study of the blood-vessels of the nerve-cord, of the oblique muscles, and of the connection between the nephrostomial and the dorsal longitudinal vessels (*D.L.V.*). $\times 3\frac{1}{2}$.

FIG. 14.—The first nephridium from the specimen shown in Fig. 13, seen from the dorsal surface, to show the gonidial vessel (*G.V.*¹) bearing blind, vascular processes. The gonidial vessel on this nephridium is sterile. $\times 4$.

FIG. 15.—Fifth right nephridium of an adult male, to show the bladder distended with spermatozoa. The nephrostome is widely open. Seen on February 24th, 1897. $\times 4$.

FIG. 16.—The second nephridium of the right side of a specimen 29.5 mm. long seen from the dorsal surface, to show the gonidial vessel (*G.V.*), the commencing processes of the dorsal lip, and the position of the external opening (*No.*²) with regard to the neuropodium (*Nm.*⁵). The ventral lip of the nephrostome (*V.Nph.*²) is seen through the dorsal one. $\times 60$.

FIG. 17.—Funnel of the first left nephridium from the same specimen as Fig. 16, seen from the right side, to show the vertical position of the nephrostome and the commencing processes on the anterior lip. $\times 90$.

PLATE IX.

FIG. 18.—The second right nephridium from a specimen 44 mm. long. Dorsal view, to show the remarkably complete capillary circulation and the extension of the vessel of the dorsal lip to form the gonidial vessel (*G.V.*). The ventral lip (*V.Nph.*²) is seen by transparency. $\times 65$.

FIG. 19.—Three views of the anterior end of a specimen 8 inches long (littoral variety), to show the prostomium, nuchal organ, openings of the otocysts, and the secondary annulation of the skin. A. From the left side. B. From above. C. From below. $\times 12$.

FIG. 20.—Transverse section across the middle of the prostomium to show the brain, the three prostomial lobes, and the rich blood-supply of this region. The brain lies in the central prostomial lobe, and its covering of ganglion-cells is closely applied to the overlying sensory epithelium. The section is cut across in the region of the posterior cerebral cornua (*P.Cr.*). $\times 65$.

FIG. 21.—Transverse section of the same series as Fig. 20, across the nuchal organ, *Nu*, the hinder cornua of the brain, and one otocyst, with its contained otoliths. $\times 65$.

FIG. 22.—Transverse section of the body a short distance behind the third diaphragm at the level of the openings of the œsophageal pouches (*GL. Op.*). The external aperture of the second nephridium is shown on the right side. The subdivision of the body-cavity into three longitudinal portions, and the structure of the œsophageal pouches, are well seen. $\times 38$.

FIG. 23.—Transverse section of the body in the branchial region at the level of a parapodium. The neuropodium is cut through its entire length on the left side. On one side of the nerve-cord a retractor muscle from the notopodium arises, on the other an oblique muscle. The vascular supply of the body-wall, setæ, and gills is well seen. $\times 38$.

PLATE X.

FIG. 24.—Amœboid and spindle-shaped cells of the cœlom. $\times 1000$.

FIG. 25.—Sagittal section of the brain slightly to the left of the middle line, from a young littoral form about 3 inches long. The mass of ganglion- and glia-cells underlying the epithelium of the prostomium is distinct; some of the cells of the latter are shown bearing sensory processes. The nuchal organ, *Nu*, is cut at its full depth. $\times 85$.

FIG. 26.—View of a dissection of the brain, œsophageal connectives, otocysts, and the buccal sheath. The commencement of the neural vessels from capillaries of the organs just mentioned, is shown. Seen from the dorsal surface. The buccal mass, cut transversely, lies in the centre of the figure. $\times 6$.

FIG. 27.—An otocyst with the otoliths composed of quartz grains. The sensory epithelium and the surrounding nerves and supporting cells are seen. $\times 160$.

FIG. 28.—Otoliths to show the chitinoid covering of the quartz grains. $\times 500$.

FIG. 29.—Ripe spermatozoon seen on March 10th, 1897. Length of head $4\ \mu$, length of tail $54\ \mu$. $\times 3000$.

FIG. 29A.—Head and portion of tail of an immature spermatozoon seen on February 22nd, 1897. $\times 3000$.

FIGS. 30—34.—Stages in the development of the spermatozoa.

Fig. 30.—The 8-celled stage, in which the spermatoblasts leave the testis. $\times 500$.

Figs. 31 and 32.—Later stages. $\times 500$.

Fig. 33.—Two cells from a stage much later than the preceding, showing the commencement of the tail. $\times 2000$.

Fig. 34.—Discoidal mass of almost ripe spermatozoa. $\times 500$.

FIG. 35.—Developing ova. (*a* and *b*) show a polar body (?) $\times 250$. (*c*) is a ripe ovum enlarged 125 times.

FIG. 36.—Longitudinal section of the heart of an *Arenicola* 250 mm. in length, to show the cardiac body. $\times 32$.

FIG. 37.—Histology of a portion of the cardiac body of fig. 36. $\times 500$.

FIG. 38.—Longitudinal section of the heart of a young *Arenicola* 65 mm. in length, to show the cardiac body at an early stage of development. $\times 50$.

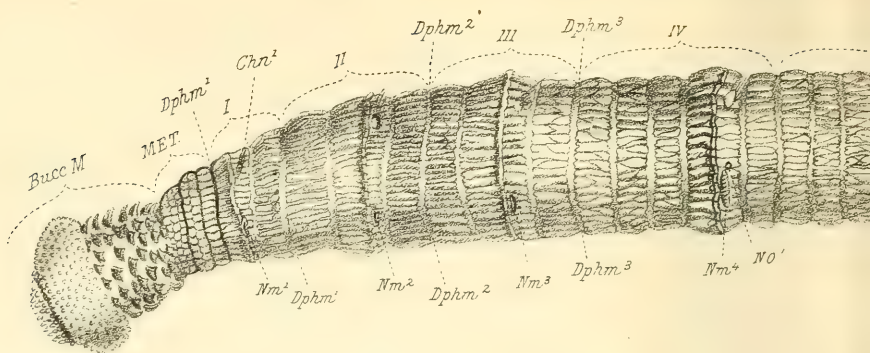


Fig. 1.

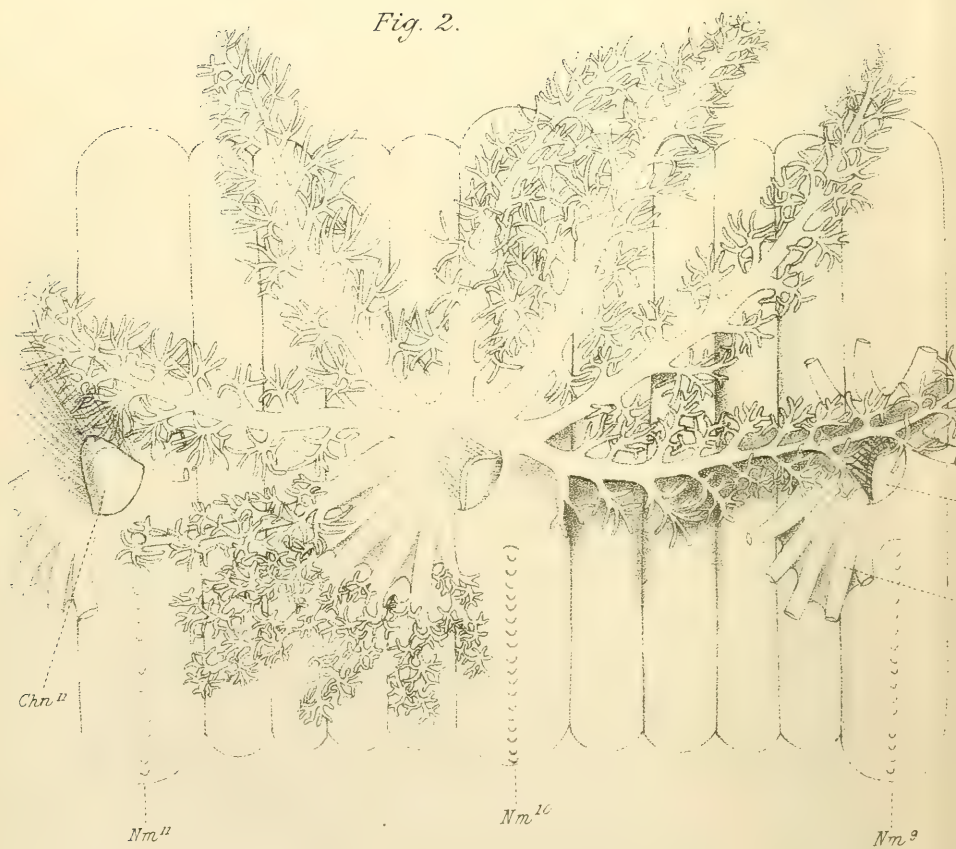


Fig. 2.

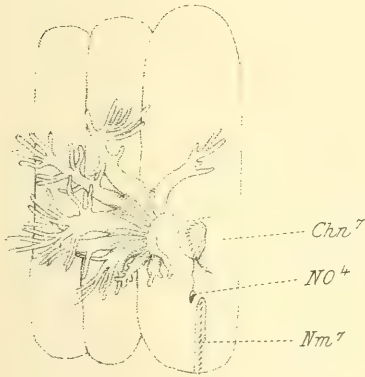
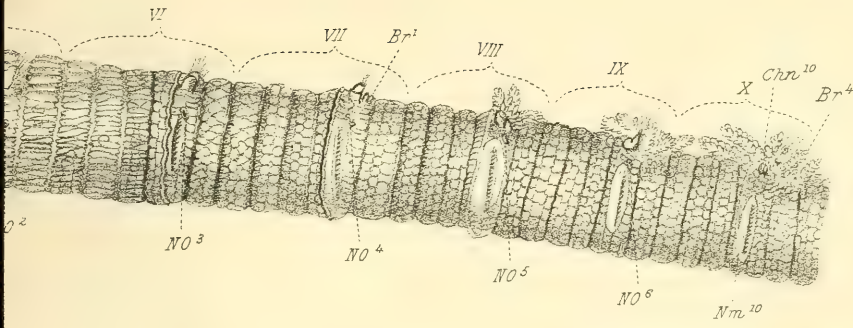
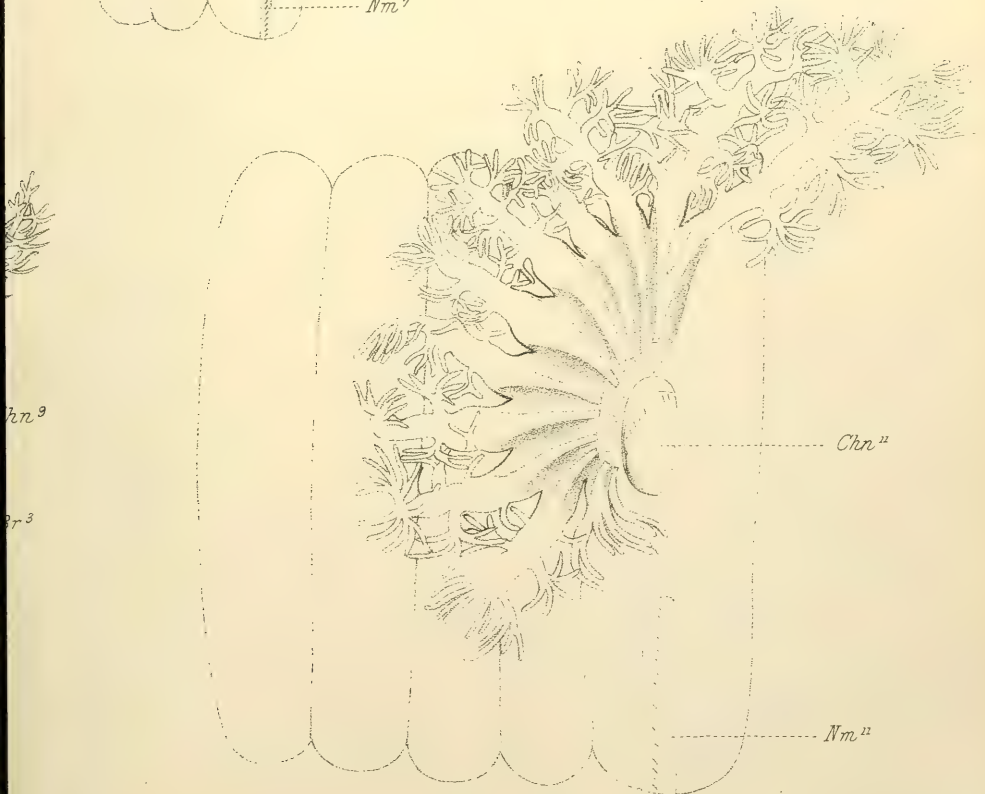


Fig. 3.







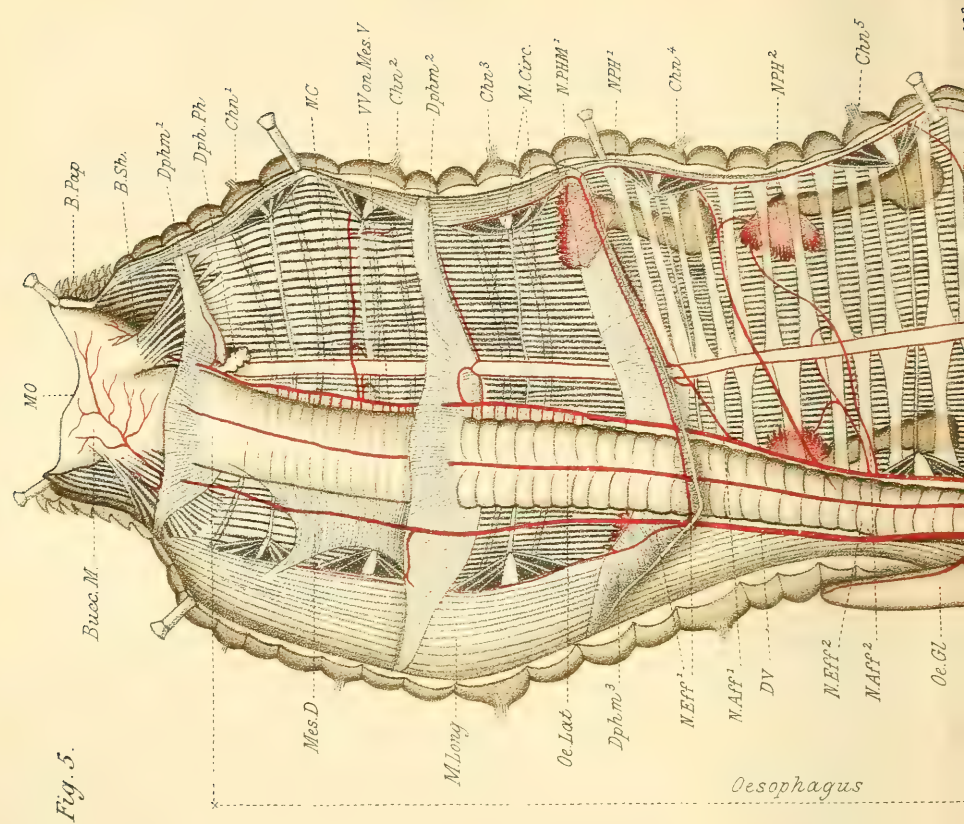
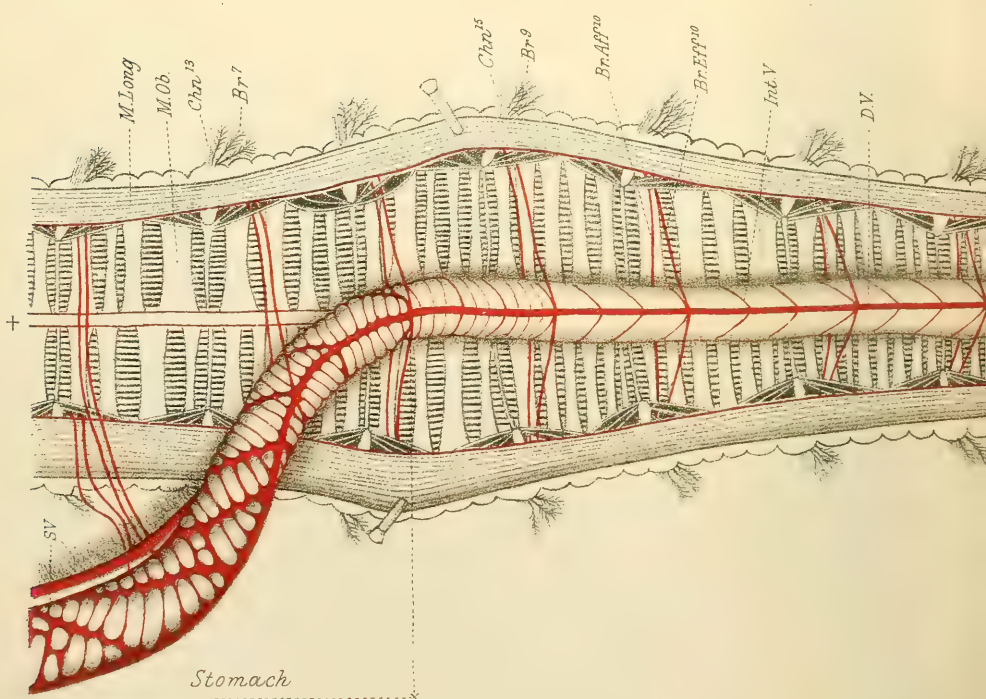
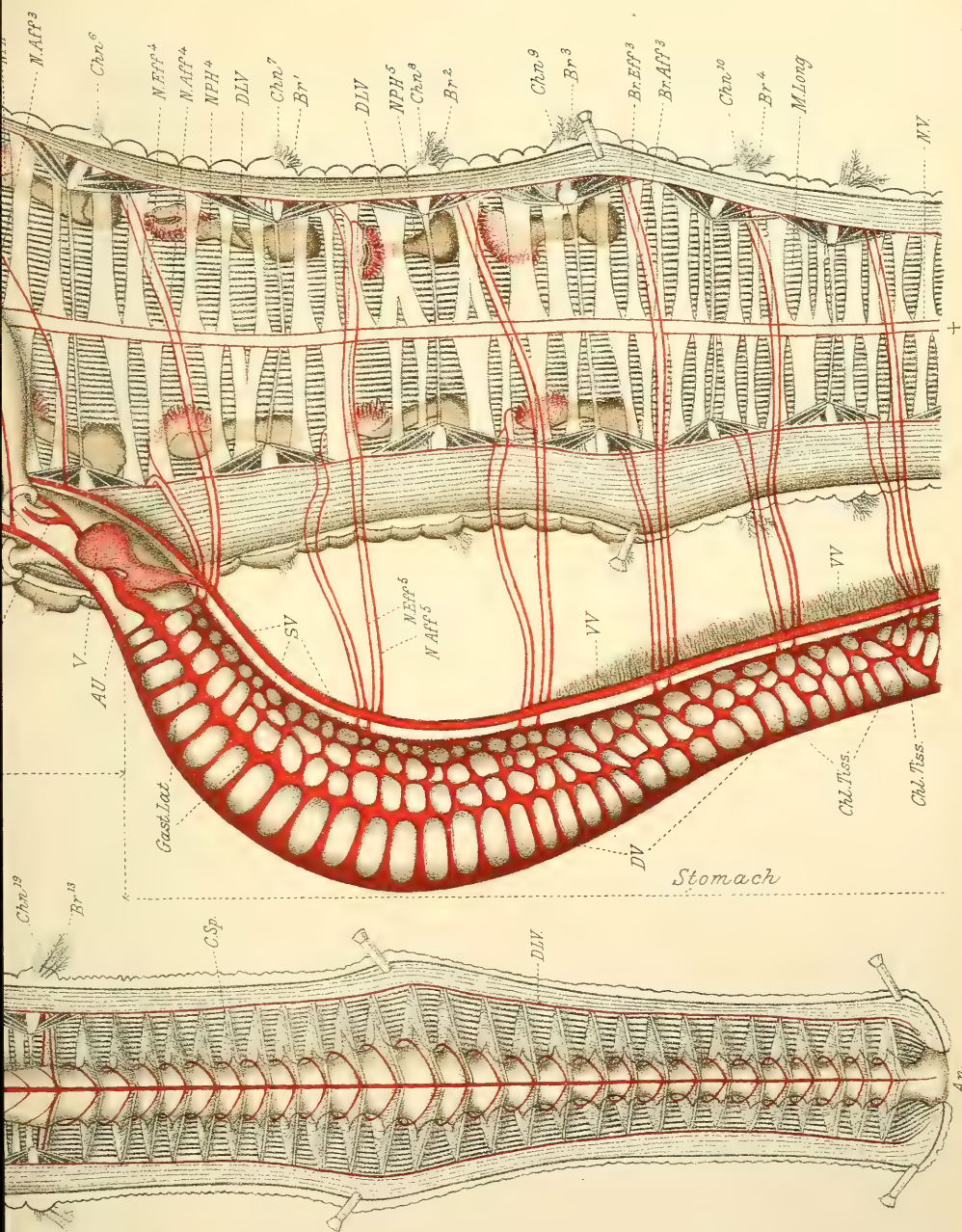
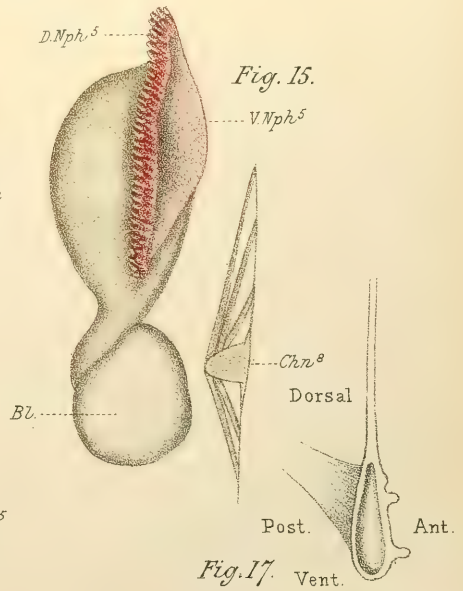
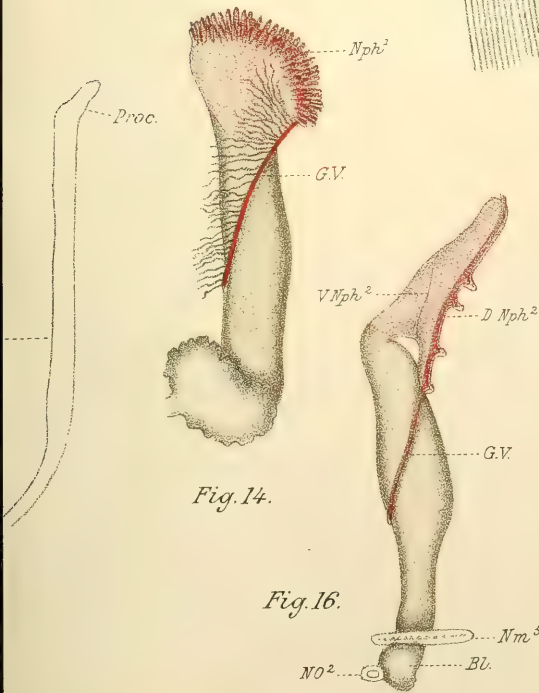
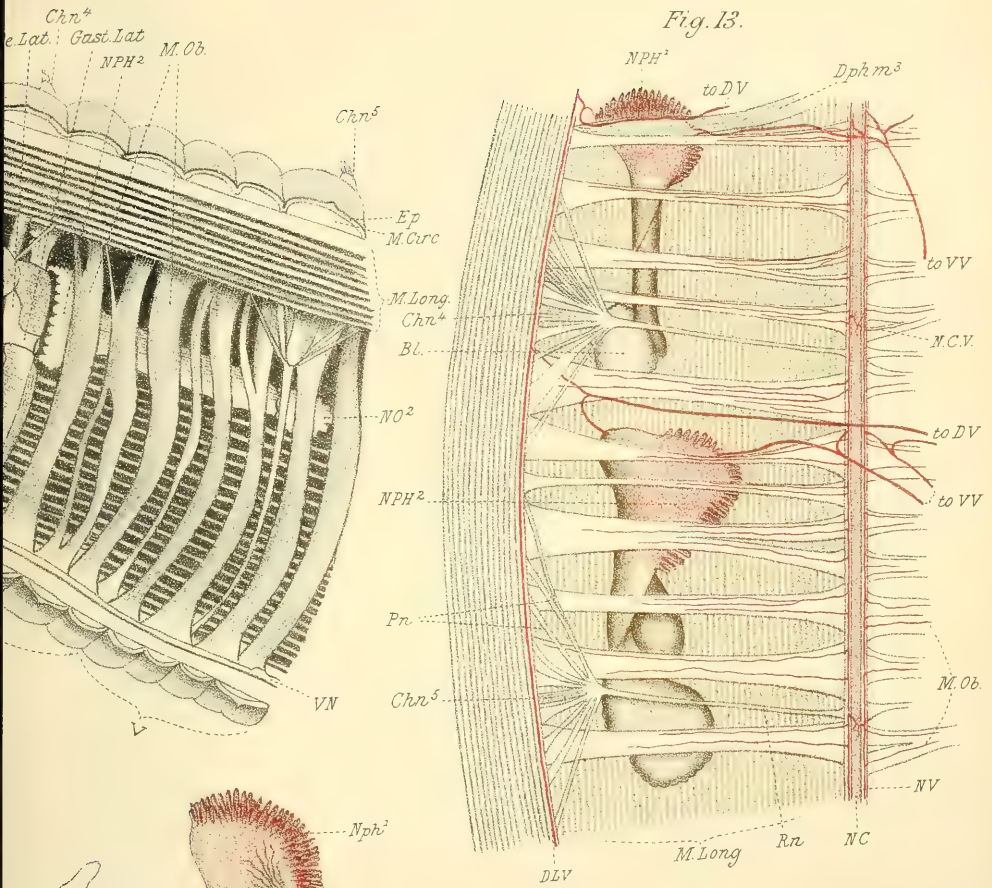


Fig. 5.









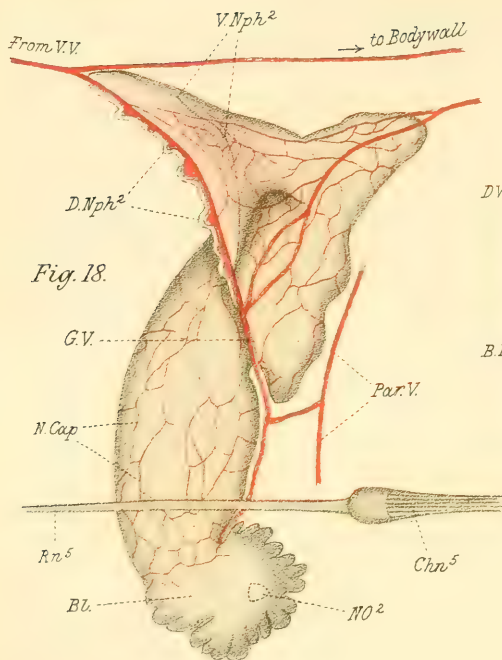


Fig. 18.



Fig. 20.



Fig. 21.

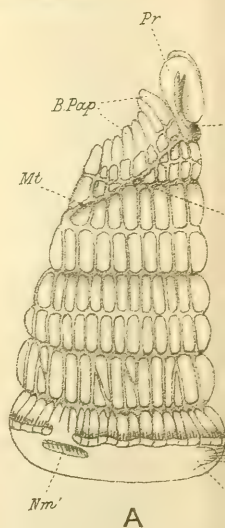


Fig. 19.

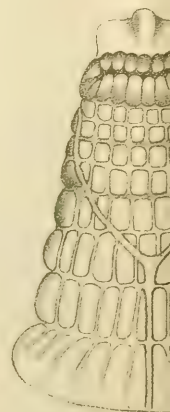


Fig. 23.

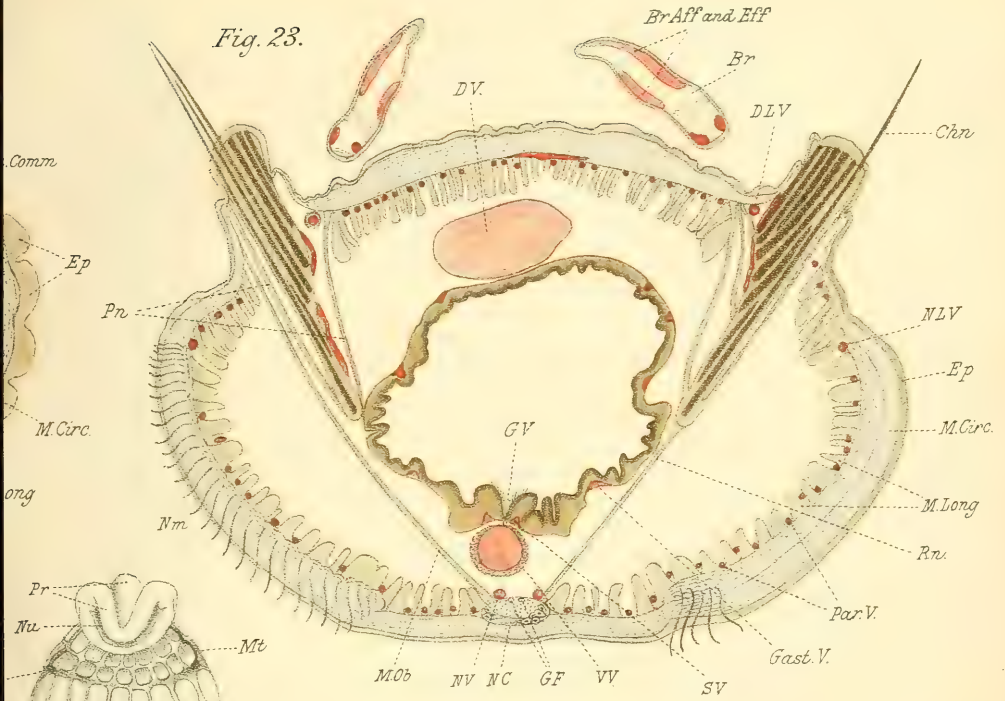
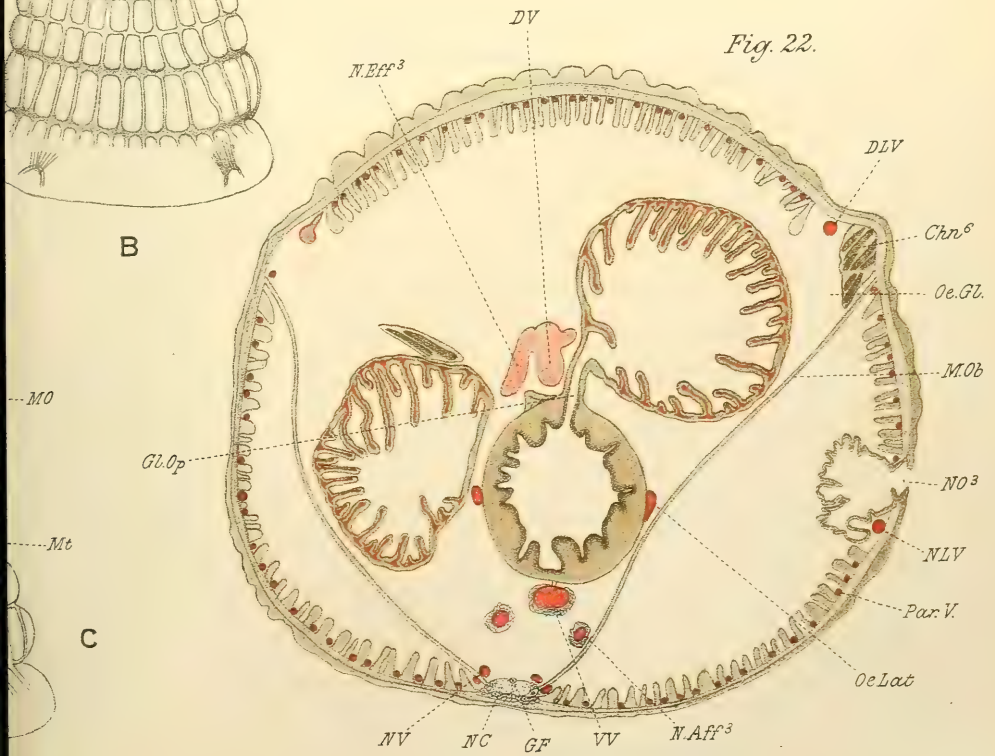


Fig. 22.



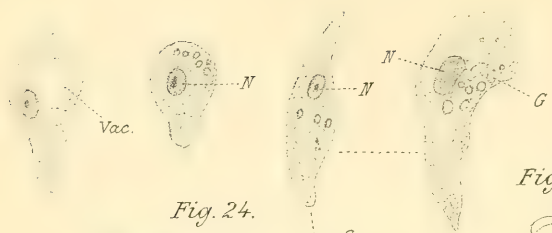


Fig. 24.

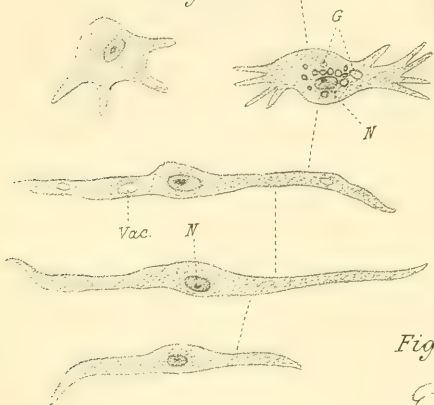


Fig. 28.

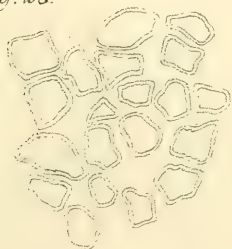


Fig. 31.



Fig. 34.

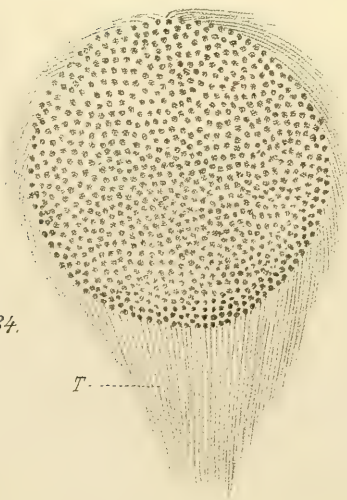


Fig. 29^A



Fig. 30.

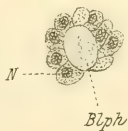


Fig. 29.

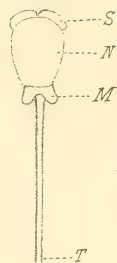


Fig. 25.

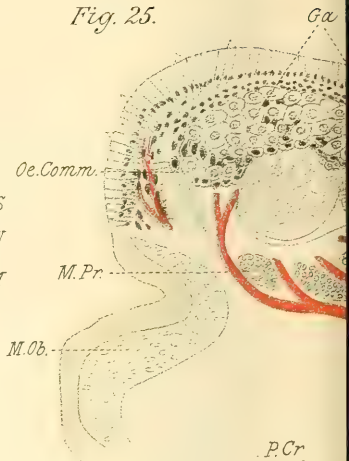


Fig. 26.



Fig. 32.

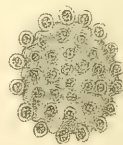
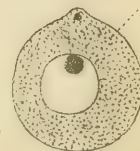


Fig. 33.



b



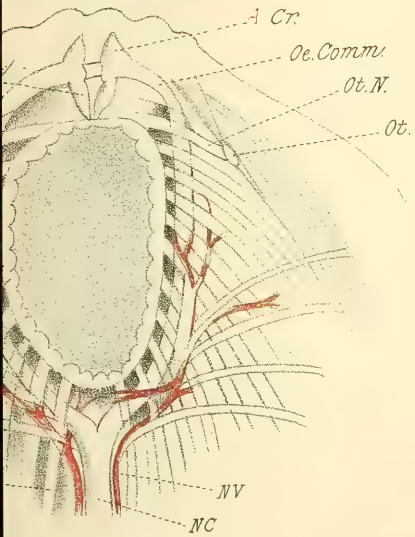
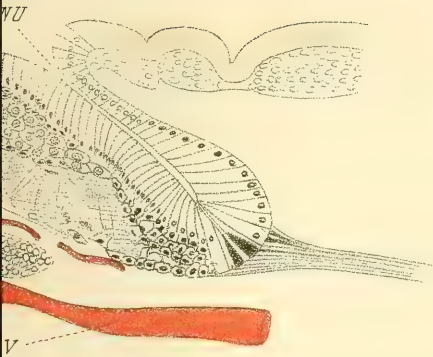


Fig. 36.

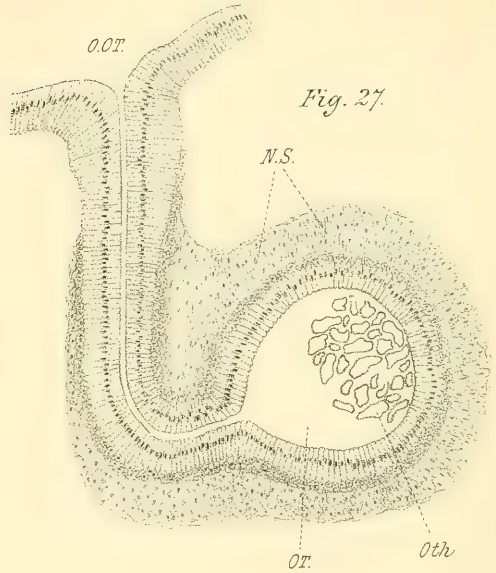
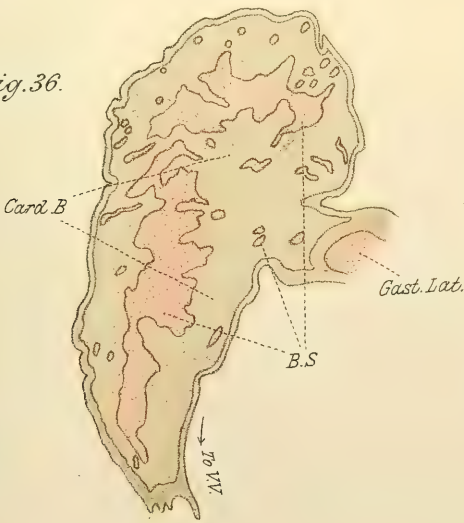


Fig. 27.

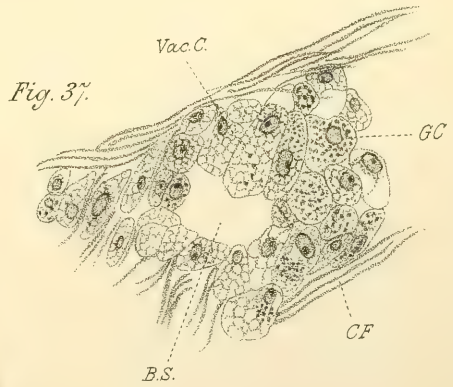


Fig. 37.

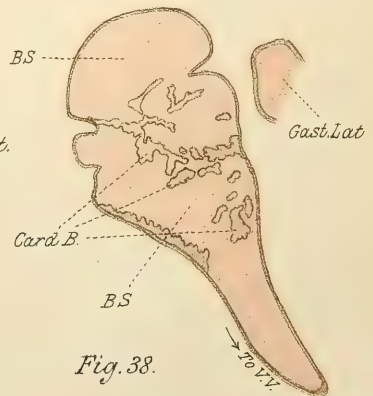


Fig. 38.

From the "ANNALS AND MAGAZINE OF NATURAL HISTORY,
Ser. 7, Vol. ii., December, 1898.

THE ENTOMOSTRACA OF LAKE BASSENTHWAITE.

By EDITH M. PRATT, B.Sc. *With an Introductory Note by* SYDNEY J.
HICKSON, M.A., F.R.S., *Beyer Professor of Zoology in the Owens
College, Manchester.*

Introduction.

The splendid researches on the character of the fresh-water fauna which have of recent years been made by Zacharias at Plön, by Birge at Mendota, and by many others abroad, serve to remind us how ignorant we are of the fauna of our own English lakes.

Investigations of the inland waters of Scotland have been conducted for some years by Scott¹; but Beck's² paper is the only one that gives a systematic account of the Entomostraca of the English lakes.

As Beck's investigations were chiefly made in the autumn months it occurred to me that it might be of interest to inquire into the character of the fauna earlier in the year, with the object of noting the principal differences that presented themselves in the early spring and in the autumn.

Accordingly in April, 1897, when the weather was still very cold, and blasts of icy wind blew down in gusts from the snow-capped Skiddaw, I took a few samples of the Plankton as a preliminary step to further investigations. The material I then obtained proved to be of considerable interest, containing among other things the interesting *Nauplius* larva of *Leptodora*.

In April of this year, the weather being decidedly warmer than in the corresponding time of 1897, I obtained the assistance of Mr. J. T. Wadsworth, and made with him a considerable number of gatherings in various parts of the Lake, so that it may be said that we obtained a fair sample of what the Plankton is at that time of year.

¹ Scott, T., Scottish Fishery Reports. Scient. Invest, 1890 onward. Invertebrate Fauna of Inland Waters of Scotland.

² Beck, C., J. R. Micr. Soc. (2) iii. p. 780.

Again, in June, with the assistance of Mr. J. H. Ashworth, B.Sc., another long series of tow-nettings were taken which show the remarkable change that takes place in the character of the Plankton during the first two months of the summer.

I have to acknowledge here my thanks to Mr. Ashworth and Mr. Wadsworth for their skilled assistance in this investigation.

As my time was fully occupied during the summer months I entrusted the duty of identifying the species to my former pupil, Miss Edith Pratt, B.Sc., of the Owens College; and the results of her investigations are recorded below.

It cannot be supposed that the list of Entomostraca which is now given as occurring in Lake Bassenthwaite is by any means complete. A complete list will be drawn up only when a series of gatherings are taken every month for two or three years; but it may be hoped that the publication of this paper will act as a stimulus for further investigation.

It is well known to fishermen that the lakes in Cumberland vary very considerably in their "trout" reputation. Bassenthwaite is not regarded as a very good lake for trout, but, on the other hand, it contains an abundance of perch and pike. It would be extremely interesting if in time a systematic study of the relations between the fish-fauna and the Entomostracan fauna could be undertaken. It would not be a very costly investigation, but it would require the whole time of a competent naturalist provided with a modest laboratory on the lake side for a period of two or three years. The results to be obtained might be of considerable value to the fishery.—S. J. H.

Bassenthwaite Lake is particularly well suited for faunistic investigations, for while being one of the lowest of the English lakes, it has the largest drainage-area; it also receives the overflow from Derwentwater and Thirlmere; therefore in Bassenthwaite we should expect to find a typical lake-fauna, and, in addition, a concentration of the forms living within the drainage-area of the lake.

Bassenthwaite¹ is the same size as Derwentwater—a little over

¹ For a complete description of Lake Bassenthwaite see 'Bathymetrical of the English Lakes,' by H. R. Mill, D.Sc.

2 square miles in area. It is 3·83 miles in length, its average breadth is ·054 mile or 950 yards. The widest part of the lake is exactly $\frac{3}{4}$ mile. The surface of the lake is 223·4 feet above the sea-level; the average depth is 18 feet: the greatest depth is 70 feet. Direct drainage-area $91\frac{1}{2}$ square miles; total catchment-area 134 square miles.

The upper end of the lake is shallow, and depths over 25 feet are confined to a trough nearly 2 miles long in the middle of the lake. The section across the lake suggests a double-troughed depression separated by a broad central rise. Mill says:—"The steep slopes of the lake above and below water were always composed of smooth rounded stones, much smaller than the great blocks of Derwentwater; the stones were only observed to be covered with mud on the shallow flats at the north-west and southern ends, and except for some rushes and water-lilies in the south-eastern corner, there were remarkably few water-plants, and no signs of a peaty floor. Well out in the lake the sediment was always found to be soft mud." The soundings were taken on June 24th and 26th, 1893.

On 4th April, 1897, a few tow-nettings were roughly made in the lake, with the view of ascertaining the nature of the fauna. The following forms were taken:—COPEPODA: *Cyclops strenuus*, and *C. signatus* were fairly common; *Cyclops affinis* was rather rare. DAPHNIDÆ: *Bosmina longirostris* and the larvæ of *Leptodora hyalina* were fairly common.

On 21st and 22nd April, and 15th, 16th, and 17th June, 1898, the investigations were more thorough, and the middle and northern portions of the lake were carefully worked at.

In April ten tow-nettings were taken, six at the surface and four at a depth of from 5 to 6 feet. The preservatives used were (1) a solution of corrosive sublimate, and (2) a mixture of formol, spirit, and osmic acid; the latter obtained better results than the former.

On 21st and 22nd April, 1898, it was noticed that the Copepods were most abundant some little distance below the surface, while the Daphnids were found in greatest numbers at the surface. The following forms were taken:—COPEPODA: *Cyclops Kaufmanni*¹ was very abundant; *Cyclops signatus* and *Diaptomus gracilis* were abundant; *Cyclops insignis*, *C. Ewarti*, and *C. strenuus*, were less abundant;

¹This form is believed to be the young male of *C. strenuus* by Mr. Scourfield, Nov. 20th, 1899.

Cyclops Thomasi was rare. CLADOCERA—DAPHNIDÆ: *Bosmina longirostris* and *Sida crystallina* were abundant; *Chydorus sphaericus* and the larvæ only of *Leptodora hyalina* were less abundant; *Bythotrephes longimanus*, *Polyphemus pediculus*, and *Daphnia pulex* were rare.

On 15th, 16th, and 17th June, 1898, sixteen tow-nettings were taken at different hours of the day at depths from 0 to about 10 feet from the surface.

This collection was characterized by the presence of the rotifer "*Asplanchna priodonta*" in immense numbers. As it occurred in the same proportion in all the tow-nettings, it must have been universally distributed.

In April the Copepods outnumbered the Daphnids, but in June the Copepods had diminished remarkably in numbers and were replaced by those Daphnids (*Bythotrephes*, *Polyphemus*, *Leptodora*, and *Daphnella*) which were rare in April.

The following COPEPODA were taken:—*Cyclops signatus* was fairly abundant; *C. phaleratus*, *C. strenuus*, *C. serrulatus* were rather rare; *C. insignis* was rare.

DAPHNIDÆ: *Daphnella brachyura*, *Leptodora hyalina*, *Polyphemus pediculus* were very abundant, with eggs, embryos, and young in various stages of development; *Bythotrephes longimanus* with eggs and embryos was abundant; *Sida crystallina* and *Chydorus sphaericus* were rare.

A few water-mites were taken which have not yet been identified.

The following species were abundant in April 1898, but were rare or not taken in June:—*Cyclops Kaufmanni*, *C. insignis*, *C. Ewarti*, *Diaptomus gracilis*, *Bosmina longirostris*, *Sida crystallina*, *Chydorus sphaericus*.

Cyclops Thomasi and *Daphnia pulex* were fairly common in April and were not taken in June.

The following species were common in June which were rare or not taken in April:—*Daphnella brachyura* (absent in April), *Leptodora hyalina* (only larvæ were taken in April), *Polyphemus pediculus*, *Cyclops phaleratus*, and *C. serrulatus* (fairly abundant, but not taken in April), *Bythotrephes longimanus*.

Cyclops signatus and *C. strenuus* were fairly abundant in April and in June.

Brief Statement of recorded Distribution in Britain of the Species taken in Lake Bassenthwaite.

ENTOMOSTRACA.

CLADOCERA.

Bosmina longirostris, Baird.

Bosmina longirostris, Baird, British Entomotraca, p. 105, tab. xv. Fig. iii.

This species appears to be fairly common and widely distributed in Britain. In Bassenthwaite it was very common in all the tow-nettings in April, but rare in June.

Sida crystallina, Straus.

Sida crystallina, Baird, Brit. Entom. p. 107.

Baird remarks that this species is of rare occurrence, but Scott records it as being common in Raith Lake in Scotland. It was the most common species taken in April 1898. In June very few specimens were taken, but these were of a large size, with well-developed ova and embryos.

Chydorus sphaericus, Baird.

Chydorus sphaericus, Baird, Brit. Entom. p. 126, tab. xvi. fig. 8.

Common in ponds and ditches in Britain almost all the year round.

Leptodora hyalina, Lilljeborg.

Leptodora hyalina, Bronn, Klass. und Ordn. des Thier., Arthrop. Crust., Erste Hälfte, Tafeln, Taf. xxi. fig. 1.

This species was first taken in England by Bolton¹ from the Olton reservoir, near Birmingham. Later it was taken by Beck in Lake Grasmere. Scott has taken it in the Scottish lakes (Loch Leven, Loch Morar), and remarks that while it is considered to be a rare species, it is not very rare in Loch Leven.

In April only the larvæ and very young forms were taken, chiefly at the surface in Bassenthwaite. In June this species was exceedingly abundant, with eggs, embryos, and young, but no young larvæ were taken. It was, moreover, confined to the middle of the lake, where the water is deep (see Map, p. 131). Very few mature specimens were

¹Ann. & Mag. Nat. Hist. (5) vol. ix. p. 53. E. Ray Lankester, "On new British Cladocera discovered by Mr. Conrad Beck in Grasmere Lake, Westmoreland."

taken at the surface, or at the depth of 2 to 4 feet; but from 6 to 10 feet (10 feet = greatest depth at which tow-nettings were taken) it was taken in great quantities.

Bythotrephes longimanus, Leydig.

Bythotrephes longimanus, Leydig, Naturgeschichte der Daphniden, p. 244, figs. 73—75, Taf. x.

British Habitat.—Scotland (*Scott*): Loch Ness, Loch Morar (frequent at surface), Loch Leven (frequent). Perthshire Lochs (*Sept.*): Loch Oich (common), Loch Tay (frequent at surface).

This species has not been recorded before from the English lakes. In Bassenthwaite it was very rare in April but very abundant in June, with eggs, embryos, larvæ, and young.

Beck describes the species "*cederstromii*" from Grasmere and other English lakes, and remarks that it appears to be more abundant in the autumn than in the spring.

Daphnia pulex, Latreille.

Daphnia pulex, Baird, Brit. Entom. p. 89, tab. xvi., fig. 5.

This species, while being widely distributed in ponds and ditches in Britain, occurs but rarely in large sheets of water; it was very rare in Bassenthwaite in April, and no specimens were taken in June.

Daphnia longispina.

Daphnia longispina, Baird, Brit. Entom. p. 91, tab. vii., figs. 3, 4.

This species was taken by Beck in English lakes and by Scott in some of the Scottish lochs. It was rare in April, and no specimens were taken in June.

Polyphemus pediculus, Straus.

Polyphemus pediculus, Baird, Brit. Entom., p. 111, tab. xvii., fig. 1; Leydig, Naturg. der Daphniden, p. 232, Taf. viii., fig. 63, Taf. ix., fig. 71.

Baird took specimens of this species in a ditch near Richmond-on-Thames; he remarks that this species seems to be very limited in its range of habitat, as he only found it in one spot not more than 20 yards in extent. Scott, however, has taken it in many of the Scottish lakes, and describes it as being a fairly common species, especially in large sheets of water; in Loch Morar, in Perthshire, it was taken by him in abundance near the surface all over the portion of the loch examined.

Beck took this species in the English lakes. It was very rare in

Bassenthwaite in April, but very abundant and universally distributed at the surface and some little distance below the surface in June, with eggs, embryos, and larvæ in all stages of development.

COPEPODA.

Cyclops signatus, Koch.

Cyclops signatus, Brady, Brit. Copep. vol. i. p. 100, pl. xvii. figs. 4—12; id. Revision Brit. Freshwater Cyclopidae and Calanidae, p. 6, pl. ii. fig. 5.

Examples with serrated and with simple ridge on antenna were taken. They are supposed to represent different stages in development (Herrick). This species is widely distributed and common in Britain.

Cyclops strenuus, Fischer.

Cyclops strenuus, Brady, Brit. Copep. vol. i. p. 104; id. Rev. Brit. Freshw. Cyc. and Cal. p. 8, pl. ii.

Widely and generally distributed in Britain, but not very common.

Cyclops Thomasi, Forbes.

Cyclops Thomasi, Brady, Freshw. Cyc. and Cal. p. 15, pl. vi. figs. 1—4.

This is not a common species. Scott has taken it in many of the Scottish lakes, but it seems to occur nowhere in great abundance. It was rare in Bassenthwaite in April, this being the first time that it has been recorded from the English lakes. No specimens were taken in June.

Cyclops insignis, Claus.

Cyclops insignis, Brady, Brit. Copep. vol. i. p. 108, pl. xxi.; id. Rev. Brit. Freshw. Cyc. and Cal. p. 18, pl. vii.

Brady describes it as being one of the less common species of *Cyclops*. I have not found it recorded from the Scottish lakes. Specimens of this species were fairly common in the middle of the lake in April, but rare in June. (I am inclined to believe now that this species is not distinct from *C. Thomasi*. Nov. 20, 1899.)

Cyclops Ewarti, Brady.

Cyclops Ewarti, Brady, Rev. Brit. Freshw. Cyc. and Cal. p. 22.

Scott has taken this species in a small bay near Queensferry, Firth of Forth. Brady remarks that this is the only undoubted member of this genus which has been found living in the sea. As it was first

found in the Forth, he thought that its habitat must be in ponds and ditches which flow into the Forth. Since then it has been taken by Scott in Loch Morar (Inverness-shire) and in Loch Moray.

Only a few specimens of this species were taken in April and none were taken in June.

Cyclops affinis, Sars.

Cyclops affinis, Brady, Brit. Copep. vol. i. p. 112, pl. xv. figs. 11—14, pl. xxiv. B, figs. 10—15; id. Rev. Brit. Freshw. Cyc. and Cal. p. 21, pl. viii.

Brady says that this species seems to be of rare occurrence. Scott records it from some of the Scottish lakes. It was taken in Bassenthwaite in April, 1897, and has not since been taken.

Cyclops Kaufmanni, Uljanin. (See note, p. 125.)

Cyclops Kaufmanni, Brady, Brit. Copep. vol. i. p. 113, pl. xxiv. figs. 6—12; id. Rev. Brit. Freshw. Cyc. and Cal. p. 24, pl. ii. fig. iii.

This species, although very limited from all accounts in its distribution, was by far the most abundant species taken in April, 1898; in June it was rare.

Cyclops phaleratus, Koch.

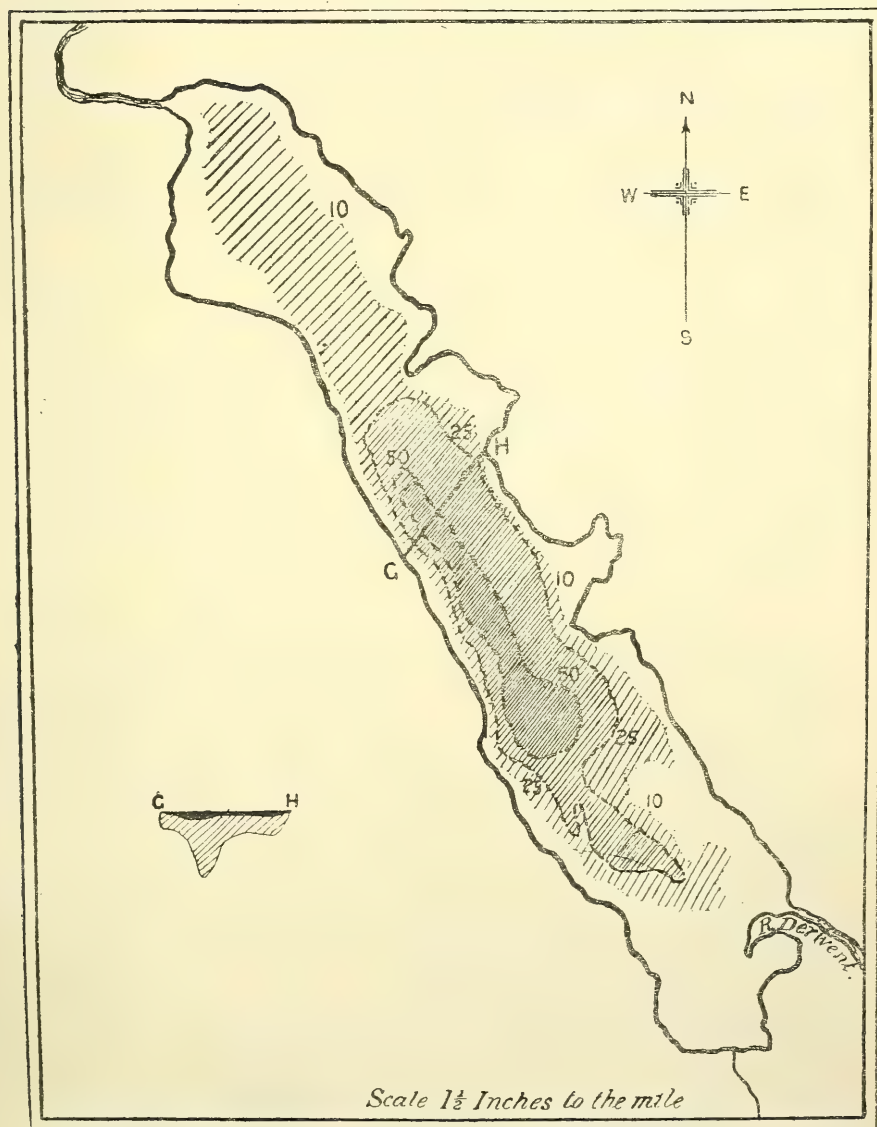
Cyclops phaleratus, Brady, British Copepoda, vol. i. p. 116.

This species is not very common, though fairly widely distributed. It has been taken in a few of the Scottish lakes by Scott, in Ireland and North of England by Brady, but has not been recorded from the English lakes. It was taken in Bassenthwaite in April, 1898, when it was rather rare. No specimens were taken in June.

Cyclops serrulatus, Fischer.

Cyclops serrulatus, Brady, British Copepoda, vol. i. p. 109, pl. xxii.; id. Rev. Freshw. Cyc. and Cal. p. 18, pl. vii. fig. 1.

This is the most common species of the genus. It occurs almost universally over Britain, and has been recorded by almost all continental writers. Specimens were only taken in Bassenthwaite in June.



BASSENTHWAITE LAKE.

(Reproduced from "Bathymetrical Survey of English Lakes," H. R. Mill, D.Sc.)

Diaptomus gracilis, Sars.

Diaptomus gracilis, Brady, Rev. Brit. Freshw. Cyc. and Cal. p. 29, pl. xi. figs. 7-9, pl. xii. figs. 1-8.

This species is universally distributed and abundant throughout Britain in large sheets of water where there is little vegetation.

(On making a revision of the material I feel doubtful if *Diaptomus castor* occurred, and I have consequently struck it out of the list. Nov. 20, 1899.)

ROTIFERA.

Asplanchna priodonta, Gosse.

Asplanchna priodonta, Gosse, Ann. & Mag. Nat. Hist. ser. 2, vol. vi. 1850, p. 18, pls. i. & ii.; Hudson and Gosse, Rotifera, p. 123, pl. xii. fig. 2.

Gosse found this species not uncommon in the Serpentine, Kensington Gardens, and in ponds and ditches near Birmingham. It was very sparingly but generally distributed in April, but in June occurred in vast quantities in all the tow-nettings taken at the surface and moderate depths.

In the Map accompanying this paper the areas of depth are signified by dotted lines.

The weather was calm and fine when the tow-nettings were made in June, but there had been heavy rains a few days before.

The tow-nettings were confined to the middle and northern portions of the lake.

In the 10-fathom area six tow-nettings were made, and were characterised by the presence of *Polyphemus* in greater numbers than elsewhere, and the almost complete absence of *Leptodora* and *Bythotrephes* (a few immature forms were taken).

In the 25-fathom area four tow-nettings were taken from 6 to 8 feet, in which *Leptodora* and *Bythotrephes* were fairly common;

In the 50-fathom area five tow-nettings were taken from 6 to 10 feet, and in these gatherings *Leptodora* and *Bythotrephes* were very abundant. (It is worthy of note that *Leptodora* and *Bythotrephes* very often occur together in great abundance.)

The remaining forms were distributed more or less universally over the portion of the lake examined.

*From the "PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON,"
April 5, 1898.*

ON THE SPECIES OF THE GENUS MILLEPORA: A PRELIMINARY COMMUNICATION.

By SYDNEY J. HICKSON, M.A., D.Sc., F.R.S., F.Z.S.

The phylum *Cœlentera* presents us with many families and orders of animals in which our knowledge of the characters which can be satisfactorily used for the purpose of systematic classification is singularly deficient. In the *Madreporaria*, the *Gorgonacea*, and the *Milleporidæ* the form of growth of the colony, the colour, and the structure of the hard skeletal parts are the only characters which have been used for the diagnosis of genera and species. In many cases it is probable that the diagnosis afforded by these characters should be considered to be satisfactory, but as the number of specimens in our museums increases it becomes more evident that in others no satisfactory classification can be framed until we have a thorough knowledge of the anatomy of the polyps which construct these skeletons and of the canal-systems which bind them together into colonies.

In some genera of *Madreporaria*, for example, of which the skeletal characters only are known, a long series of intermediate stages can be found between the type specimens of the different species, and every new collection of specimens that is examined increases the difficulty of deciding whether a particular intermediate form belongs properly to one species or another. Moreover, in this same group the outlying species of one genus resemble the outlying species of another so closely that it is often a matter of great difficulty to determine, on our present system, to what genus a particular specimen belongs.

Nearly every important systematic work on these *Cœlenterates* contains some remarks about the difficulty of determining species, and examples are quoted of series of intermediate forms connecting closely allied species. If it were possible to frame some general rule for the

correct definition of a species, which would be agreed to by all systematic zoologists, our task might be less difficult than it is; but, as matters stand, the conception of what is a species of one worker is so different from that of another that there is constantly going on a seesaw of construction and destruction of new species in our systematic literature.

I do not propose to attempt to define the conception "species" in Cœlenterates, but I think that all zoologists would agree that, if a form which is known as species A were proved to give rise to an embryo which grew into a form which had hitherto been known as species B, the two forms would have to be merged into one species with one specific name. Similarly, I imagine that all zoologists would agree that if a coral known as species X changed in the course of its life-history into a form known as species Y, then the forms X and Y should be regarded as one species and retain only one name. In the absence of any experimental proof that the embryo of one so-called species of coral gives rise, under any circumstances, to another so-called species, or that one so-called species changes in the course of its life history into another, it is necessary to examine with very great care the anatomy of the soft parts as well as the skeletal structures, in order to determine whether it is possible or even probable that such changes actually occur in nature. If we find, then, that the polyps or reproductive organs of a coral with one form of growth are essentially different from those of another form, we may consider there is good reason for believing that such changes do not occur and the species founded on the skeletons are good; but if, on the other hand, the polyps, reproductive organs, and other characters of the two forms are essentially the same, then there is reason for believing that the species founded on skeletal characters may not be good.

Before proceeding further with this discussion of the characters which may be used for distinguishing species in Cœlenterates, it may be well to describe briefly the general results of my observations on the genus *Millepora*. This genus stands quite by itself among living corals. No one genus of the other Hydrocorallines can be confused with it, both the living tissues and the hard skeletal parts being perfectly distinct. It is widely distributed through the tropical seas, occurring in the Red Sea, Indian Ocean, Malay Archipelago, Tropical Australian waters, Pacific Ocean, and in the seas of the West Indies. It is essen-

tially a shallow-water genus, living in abundance in most of the coral-reefs, and not occurring in greater depths than 15 fathoms.

The form varies immensely. It may be broadly lamellate or densely branched, or anastomosing, or it may form thin incrusting plates on dead corals. In all large collections of Millepores series of intermediate forms may be found between all the most prominent types.

The difficulty of defining and describing the species of this genus has been commented upon by several authors. Dana, for example, says "There is much difficulty in characterizing the Millepores on account of the variations of form a species undergoes and the absence of any good distinctions in the cells. The branched species are often lamellate at the base, owing to the coalescence of the branches, and the lamellate species as well as the branched sometimes occur as simple incrustations." My own investigations confirm and amplify Dana's statement on this point.

Notwithstanding these difficulties a large number of species of the genus have been described. In the writings of the older naturalists many species were described which have since been relegated to other classes of the animal kingdom, and in palæontological literature we find many species of fossil corals referred to the genus on erroneous or very unsatisfactory grounds.

Apart from all these, which may be left out of consideration in this paper, no less than 39 species of the genus *Millepora* have been described.

The characters which have been used for determining these species are :—(1) The form of the corallum. (2) The size of the pores. (3) The degree of isolation of the cycles. (4) The presence or absence of ampullæ. (5) The texture of the surface of the corallum.

(1) *The Form of the Corallum*.—This feature is even more unsatisfactory than I anticipated at the beginning of my investigation. In the first place, attention has been called by Dana, Duchassaing and Michelotti, and others to the fact that *Millepora* grows in an incrusting manner on many objects, and thereby assumes the form of the object on which it grows. It is quite easy to distinguish such forms as incrusting forms when they have only partially covered such objects as the horny axis of a *Gorgonia*, a glass bottle, or an anchor ; but in many cases the object is so completely overgrown by Millepore and other marine zoophytes that its presence is not discovered until a fracture is

made. To give only one example to illustrate this point :—A specimen in the Manchester Museum was named *Millepora intricata*, and, on comparing it with the description of the species, I thought at first that the name was correct. On breaking it into two pieces, however, I found that the form it had assumed was due to the fact that it had grown over a small piece of wood.

In a still greater number of cases, however, the Millepores grow upon the dead coralla of other Millepores or Madreporae or other white corals, and then the difficulty of determining whether the form of the specimen is due primarily to the living coral or to the one on which it has grown becomes extreme. There is a large specimen in the collection brought home from New Britain by Dr. Willey, of very irregular form, one part of which has a form like that attributed to the species *M. plicata*, another part to the species *M. verrucosa*, but a broken knob shows quite clearly that a part of this great mass has grown over a dead coral. It would consequently be quite impossible to determine with any degree of satisfaction to which of the already-described species it belongs, unless every knob and projection were broken off to see whether the dead coral extends as a basis through the whole piece.

In the second place, the immense amount of variation in form which occurs in large specimens of *Millepora*, and, indeed, in many small specimens too, leads to very great difficulties in the determination of species which have been described on form as the principal character. In Dr. Willey's collection there is a series of varieties of growth leading from a massive lamellate form to a complicated branching and anastomosing form.

A careful study of these skeletons, then, points very definitely to the conclusion that the general form of the corallum of *Millepora* should be used, not as a primary, but as a very subsidiary character in the description of species.

The form assumed by the corallum must depend upon many circumstances connected with the exact spot on which it grows. If a *Millepora* embryo happens to become fixed on a large piece of dead coral, it will form a large incrusting base, and such a base nearly always gives rise to a lamellate form of growth ; if, on the other hand, the embryo settles on a small stone or other object, lamellate growth is impossible, and the corallum will be ramified.

The growth of the corallum must also be influenced by the propinquity

of other corals. Its form must be adapted to the space left between its neighbours on the crowded reef. Again, its form must be modified by the depth of the water in which the embryo happens to develop. As Duchassaing and Michelotti pointed out long ago, *Millepora* often grows in very shallow water and is consequently unable to develop in height. Specimens that happen to fix themselves on foreign bodies on the edge of the reef at a depth of 5 or 6 fathoms can and do grow to a very great length without impediment.

It is also extremely probable that the available food supply, the particular set of the tides and currents, and the chemical composition of the sea-water, particularly as regards the amount of calcium carbonate it holds in solution, vary very considerably in different reefs and in different parts of the same reef. Such variations must affect the rate of growth of Millepores, and I think it is reasonable to believe the mode of growth also.

(2) *The Size of the Pores*.—Dana, Milne-Edwards and Haime, and Quelch have used the size of the pores as a specific character, but, with one exception, to be referred to presently, they give no measurements, being contented to use the expressions "very small," "large," "minute," &c. Unless the zoologist has an immense number of specimens from different localities to compare one with another, it is difficult for him to understand what is meant by such expressions; but even the naturalists of the great national collections would be mystified by the case of *M. alcicornis*, whose gastropores are, according to Quelch, very large, and according to Milne-Edwards and Haime, "très petits." I have measured a very large number of gastropores, taking for each specimen an average of 6 or 12.

The greatest average diameter of the gastropores I have found is 0·37 mm., the smallest is 0·13 mm., so that the difference between those pores which might legitimately be called "very large," and those that are "very small" is 0·24 mm. But these "large" pores are very rarely seen; the great majority of the gastropores are between 0·3 mm. and 0·2 mm. This general result agrees fairly well with the only measurement I have been able to find in the literature of the subject, namely, that of *M. murrayi* by Quelch, which is given as 0·25 mm.

The question that had next to be considered was whether there is any other feature constantly associated with large pores and with small

pores. The large pores are very constantly found in specimens with thick lamellæ or branches, while the small pores are found on those of a more slender habit.

A further investigation of the question yielded an explanation of the variation in the size of the gastropores, which proves that it cannot be of any real service for specific distinction.

I found that in the gastropores of specimens of slender growth there are only 3 or 4 tabulæ, while in those of more massive growth there may be as many as 9 or 10 tabulæ. This suggested that the size of the gastropore depends upon the age of the gastrozoid which lived in it, and, on measuring carefully a number of gastropores from the base, middle branches, and growing-points of a specimen in the Manchester Museum labelled *M. complanata*, I found that the average diameter of the gastropores at the base, which we may assume in this case to be the oldest part, was 0·185 mm., on a middle branch 0·17 mm., and at the growing-edge, *i.e.*, the youngest part, it is only 0·13 mm. This general result was confirmed by similar series of measurements on other specimens. I also found that the greatest average diameter of gastropores which I have given above was obtained from the base of a massive specimen, while the smallest was obtained from a growing-edge of a slender specimen.

Moreover, it occurred to me that if the size of the gastropores is dependent upon their age or the rate at which the gastrozoids have grown, there ought to be, in some cases at any rate, a difference between the average size of the gastropores on one side of a branch or plate and that on the other; those on the face most favourable as regards food supply in the living state should be larger than those on the other. Measurements confirmed my point, and I found a difference in two out of three specimens between the gastropores on one side and those on the other as great as 0·03 mm.

(3) *The Degree of Isolation of the Cycles*.—Moseley noticed that in one specimen of Millepore taken at Zamboanga the cycles were much more distinct than in other specimens, and suggested that this feature might be of specific value. After very careful consideration I am convinced that it cannot be. In many large specimens it will be seen that the cycles are much more distinct in one part than another. Sometimes the cycles are so crowded as to be indistinct at the edge, and perfectly clear on the face or at the base. The evidence points to the

conclusion that in slow-growing Millepores in unfavourable situations the cycles are distinct, and that in fast-growing specimens in good situations the polyps are formed in such great numbers that the cycles become confused.

(4) *The Presence or Absence of Ampullæ*.—The ampullæ of *Millepora* were discovered by Quelch in a specimen obtained by the 'Challenger.' He found a new species for the specimen, which he called *M. murrayi*, and used this feature as an important specific character.

I have found that ampullæ occur in plicate, ramose, and digitate specimens, and, as will be explained later, the absence of ampullæ in any particular specimen merely means that at the time it was taken it was not in a state of sexual activity.

It is greatly surprising how very rarely specimens are found in this particular condition, but I believe that it must occur in all varieties at one time or another in their life-history.

(5) *The Texture of the Surface of the Corallum*.—The species *M. verrucosa* of Milne-Edwards, *M. tuberculata* of Duchassaing, and *M. striata* of Duchassaing and Michelotti have been named after the peculiarities of their surface.

I have had an opportunity of examining a very fine specimen of a Millepore, resembling very closely the type of *M. verrucosa*, and I found that on the summit of a very large number of the verrucæ there is a small hole of the shape of a keyhole, which leads into a cavity formed by a parasitic cirripede (probably *Pyrgoma milleporæ*). On others, however, no such evidence of parasitic interference with normal growth is apparent from the surface, but nevertheless there is reason for believing that the tubercle may have been due to hypertrophy of the Millepore at a spot which was irritated by some parasite, the parasite subsequently being overwhelmed or killed.

Now it is not cirripedes alone which attack Millepores; various algæ, worms, crabs, and other creatures settle on the Millepores and cause profound modifications of their growth.

I think there is very good reason for believing that the warts, tubercles, ridges, and the like which occur on the surface of these corals are primarily due to parasites or to some other irritant, and that it is very doubtful whether they are ever of specific value. If they are to be used, however, it will be found that they lead to many difficulties, as it is not infrequently the case that one side of a lamella is tuberculate

and the other is not, or that one lamella or branch is covered with wart-like processes and the others are smooth.

(6) *The Relative Number of Dactylopores and Gastropores*.—Finding that all other characters derived from the skeleton are unsatisfactory for determining and distinguishing species, I thought it possible that a good character might be found by calculating the average number of dactylopores to each gastropore in a number of species.

In many specimens the cycles are so close one to another that it is often difficult to determine to which cycle a particular dactylopore belongs. In order, therefore, not to be misled, I used only those cycles which were clearly defined from their neighbours.

In the following table I have put together the results of my calculations on this point:—

Accepted specific names of specimens. (The name of donor and locality in parentheses.)	Number of cycles counted.	Average No. of dactylopores in each cycle.	Highest number.	Lowest number.
I. <i>M. murrayi</i> . (Haddon, Torres Str.)	6	5·15	8	5
II. <i>M. alcornis</i> . (Brit. Mus., W. Indies.)	8	6·45	8	5
III. <i>M. alcornis</i> . (Shipley, Bermudas.)	6	5·6	7	5
IV. <i>M. alcornis</i> . (Lister, Tonga.)	12 12	6·7 5·08	8 8	6 3
V. <i>M. plicata</i> . (Hickson, Celebes.)	12	7·08	9	6
VI. <i>M. complanata</i> . (Man. Mus., W. Indies.)	7 100	6·28 5·82	7 7	5 4
VII. <i>M. alcornis</i> . (Man. Mus., W. Indies.)	7	6·14	7	5
VIII. <i>M. alcornis</i> . (Agassiz, Bahamas)	13	5·5	9	4

It will be seen from these figures that there is not much variation in the average proportion of dactylopores to gastropores in the different forms examined. The largest number of cycles I was able to count on one colony gave an average of a trifle under 6. It is noteworthy that this is the exact mean of the highest and lowest averages obtained from smaller specimens on which only a few cycles could be counted.

The extreme averages 5·08 and 7·08 (IV. & V.) do not show so great

a range as may be seen on different parts of a single piece 9 and 4, and 8 and 3.

On the basal incrusting regions of a specimen of Millepore in the Manchester Museum I have observed several widely-separated gastropores attended by only one, two, or three dactylopores, and a similar paucity of dactylopores I have more recently noticed in specimens from the collection made by Mr. Gardiner in Funafuti and Rotuma.

I may point to the figures obtained from an examination of the specimens of *M. alaicornis* given to me by Mr. Lister to show the variability of this feature in the colony.

The specimens were a number of broken branches, each a few inches in length, beautifully preserved in spirit. Two specimens were taken at random and twelve cycles counted on each. The average of one came out 6·7 dactylozooids to each gastrozooid, and of the other 5·08 dactylozooids to each gastrozooid.

The only author who has referred to the number of dactylopores in each cycle is Moseley. He says that each group consists "of a centrally placed gastropore surrounded by a ring of five, six, or seven dactylopores," and on counting the number of dactylopores in each cycle that are drawn in Mr. Wild's picture in Moseley's 'Philosophical Transactions' paper I find that the average is 6.

In Milne-Edwards and Haime's figure of *M. intricata* there are 5 gastropores to 35 dactylopores; of *M. verrucosa*, there are 7 gastropores to 32 dactylopores (?); in *M. tuberculosa*, 5 gastropores to 18 dactylopores; but it is not certain that these figures can be absolutely relied upon. They are, however, on the whole, very similar to my own results.

The general conclusions, then, that must be drawn from these observations are :—

That the number of dactylopores in each group is very variable in each individual colony of *Millepora*. There may be, in fact, any number up to 8 or 9.

That specimens of widely different forms of growth have approximately the same average number of dactylopores in each group.

That the average number of dactylopores, in each group for specimens of all kinds is about 6.

That the average number of dactylopores to each gastropore cannot be used as a specific character.

Anatomy of the Soft Parts.—I have examined the anatomy of the soft parts of a large number of specimens preserved in alcohol by mounting them whole and by making series of vertical sections. The following is a list of the specimens examined :—

<i>Form of growth.</i>	<i>Donor.</i>	<i>Locality.</i>
Digitate & palmate.	Prcl Haddon.	Torres Strait.
"Alcicornis."	Mr. Shipley.	Bermuda.
"Alcicornis."	Mr. Lister.	Tonga.
"Alcicornis."	Prof. Agassiz.	Bahamas.
"Alcicornis."	British Museum.	W. Indies.
Ramose.	Mr. Gardiner.	Funafuti.
Plicate,	"	"
Foliate.	"	"
Striate.	"	Rotuma.
Ramose.	Dr. Willey.	New Britain Group.
Plicate.	"	"
(Several small fragments).	"	"
Complanate.	Mr. Duerden.	Jamaica.
"Exaesa."	Dr. von Marenzeller.	Red Sea.
"Dichotoma."	"	"

And a specimen of "Plicate" form obtained by myself in Celebes.

The preparation and examination of these Millepores has extended over a period of twelve years, with the result that I have failed to find any constant difference between them that can be used for the separation of the genus into species.

The structure of the gastrozooids and the dactylozooids is essentially the same in all the specimens examined, but the size varies somewhat, according to the position from which the preparations are made—those at the growing-edges being smaller than those at the base, &c. The canal-system is the same in all specimens. *Zooxanthellæ* of exactly the same size are always present in the superficial canals. I have observed the two different kinds of nematocysts, the large and small figured by Moseley, in all my preparations. Many of the Millepores are known to sting badly, and have received popular names in various languages expressive of this feature, but Mr. Gardiner informs me that one form in Funafuti did not sting. "It was at its base

rather overgrown by weed, and above, curiously enough, it did not sting, and was the only one in Funafuti that did not."¹

It is not known whether both the large and the small nematocysts possess the stinging-power, or whether it is confined to only one kind. The small nematocysts are confined to the tentacles of the gastrozooids and dactylozooids, and the large nematocysts, when ripe, occur in the superficial coenosarc between the pores, but are specially crowded in the neighbourhood of the gastropores. Moseley's description of these features in *Millepora* is correct for all specimens I have examined. The size and the position of the small nematocysts render them difficult to measure, but the large nematocysts can be scraped off the surface of any preserved specimen in considerable numbers. The average size of these nematocysts when ripe in specimens from Celebes, Bermuda, Bahamas, Funafuti, Rotuma, the Red Sea, Jamaica, and New Britain is exactly the same—0.02 mm. $\times$ 0.025 mm. The number of the nematocysts varies considerably, but as this must be influenced by the manner in which the specimens were killed, and by external conditions affecting them before they were killed, no differences of specific value can be framed from this feature.

The general anatomy of all these forms is in other respects, as well as those mentioned, so much alike that I know of no means of distinguishing one series of sections of well-preserved material from another. There are no features of the soft parts which indicate in the least the general character of the form and structure of the skeleton they secreted.

By far the most interesting and in many respects the most important structures of these corals are the generative organs, and to them we should naturally turn for characters which might assist in distinguishing species. Unfortunately, however, our knowledge of these structures is very meagre and does not at present help us very much.

In the specimen presented to me by Prof. Haddon from Torres Strait, I discovered that the male sexual cells migrate into dactylozooids which become converted into medusæ. These medusæ, when ready to become free, are situated in ampullæ, which are approximately 0.4 mm. in their greatest diameter: that is, in holes in the skeleton larger than the largest gastropores. In another specimen of a different mode of growth presented to me by Mr. Gardiner from Funafuti I found numbers

Extract from a private letter.

of these medusæ in ampullæ of exactly the same size. The medusæ of these two forms are quite indistinguishable one from another. It seems probable, then, that the Millepores from Zamboanga (Quelch), Jamaica, and several others from unknown localities in which ampullæ of this character have been described bore in the living state medusæ. No gaps similar to these can be seen in any of the preserved specimens which have been examined except those which contain or have contained medusæ. The fact that the largest ampullæ of all specimens are of approximately the same size, coupled with the fact that the medusæ of such different forms as those given me by Mr. Gardiner and Prof. Haddon are exactly similar, suggests that the medusæ of all Millepores are similar. At any rate, there is no evidence at present that there is any difference between the medusæ of the different forms.

It is a very extraordinary fact that the ampullæ are so rarely found. I have had the opportunity of examining carefully a very large collection of Millepores collected in the West Indies, and deposited in the Liverpool Museum. I failed to find a single ampulla in any one of them, but a small skeleton sent to me by Mr. Duerden from Jamaica exhibited an immense number of them. In the large collection at the British Museum only a few specimens exhibit ampullæ.

It seems to be certain, then, that the medusæ are but rarely formed, but when they are they are formed in very great numbers.

General Considerations.—It appears to me that these investigations present very strong reasons for believing that there is only one species of *Millepora*. That one species must, on the ground of priority, be called *Millepora alaicornis*.

There are two courses open to us: either to assume that there are characters still undiscovered which distinguish one species from another, and on the strength of that assumption retain the old specific names; or to wait until such assumed characters are discovered before recognizing more than one species.

Of these two courses the latter appears to me to be preferable. If we consider a series of specimens; *a*, *b*, *c*, *d*, &c., are distinct species, we assume that the embryo of *a* gives rise to a definite form of coral, so like its parent *a* that it can be easily distinguished from the forms *b*, *c*, *d*, &c. If, on the other hand, we consider them as modifications in the form of one species, then we may consider it possible that under different external conditions the embryo of *d* may give rise to a form

similar to *b*, or *c*, or *d*, or any intermediate or combined form of these varieties.

By the former course we are practically denying the possibility of considerable plasticity; by the latter course, while not assuming that it exists, we do not deny it.

Now the evidence in favour of the view that the Millepores are extremely plastic in their growth increases with every new collection that is examined. Nearly every large specimen shows some branch or plate that is distorted, twisted, compressed, or bent into a different shape from the rest of the coral; its surface shows galls, cups, tubes, warts for the accommodation of crabs, worms, cirripedes, algæ, and other so-called parasites. Nor is there any greater constancy of form in the smallest independent specimens that can be found. They may be simply incrusting, or may form a simple crest, or a short pointed process from the base, according to the character of the object on which they grow. It is therefore, in my opinion, not only extremely inconvenient, but positively erroneous, to consider those forms of growth that may be grouped round one "type" as a species distinct from those that can be grouped round another "type." By this plan we either deny the extreme degree of variability which there is reason to believe does occur in nature, or else we employ specific names in a sense altogether different from that in which they are used in the other groups of animals and plants.

It would be premature to propose to extend my remarks to other genera of corals, but I have already pointed out that there are some reasons for believing that there is not more than one species in the Alcyonarian genus *Tubipora* and the Hydrocoralline *Distichopora*. Our knowledge of the soft parts of *Madrepora* and other genera of Zoantharian corals is so small that it is possible that in the future a very considerable reduction in the species of this genus will also be necessary. *Madrepora* itself is a genus with a very wide geographical distribution in shallow tropical waters, like *Millepora*. Its coralla are also subject to extraordinary variability in their form of growth, and the species have been founded on skeletal characters only. All the species, or many of them, may be good, but the classification of the genus must be considered to be unsatisfactory until our knowledge of the anatomy of the polyps of the different varieties has been considerably extended.

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CRAB-GALL ON MILLEPORA.

By SYDNEY J. HICKSON, M.A., F.R.S., *Beyer Professor of Zoology,*
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With Plate XI.

The occurrence of gall-like growths on certain genera of branched Zoantharian corals, belonging to the genera *Sideropora*, *Seriatopora*, and *Pocillopora*, has been known to zoologists for many years. The best description of them may be found in Semper's interesting book, "The Natural Conditions of Existence as they affect Animal Life."¹

The Crab that causes the growth of the gall is called *Hapalocarcinus marsupialis*. These galls are by no means rare. In nearly every Museum which possesses several specimens of these genera, examples of such galls are sure to be found; and in *Seriatopora* itself as many as nine or ten galls in different stages of formation are frequently seen in specimens less than a foot in diameter.

The occurrence of Crab-galls on *Millepora*, however, has not, I believe, been hitherto recorded. It must, however, be of extremely rare occurrence, as it has never before come to my notice. During the past ten years I have examined the whole stock of Millepores in several Museums, and have received for examination from naturalists in various parts of the world the specimens of this genus that they have collected. I have noted the various parasites and commensals that are found on them, and the many variations and distortions of growth that they exhibit, and, therefore, have good reason for saying that the occurrence is a rare one.

¹ Kegan Paul, *International Scientific Series*, 1881.

On the specimen in the Derby Museum, Liverpool (Fig., p. 80), there are three galls, two complete and one in process of formation.

Of the three galls the lowermost (*a*) in the figure is the oldest. It is about 30 mm. long by 25 mm. broad, and the aperture is oval, 8 mm. by 6 mm. in size.

The cavity is large, its diameter being considerably greater than the greatest diameter of the aperture. The dried crab remains in this gall, but as it would be impossible to extract it without injury, I am unable to say more about it than that it is very much smaller than the cavity in which it lives.

The second gall (*b*) is smaller and much more spherical in shape, its diameters being approximately 20 mm. The aperture is relatively larger than that of the other, being 6 mm. by 7 mm. in size. It contains no crab.

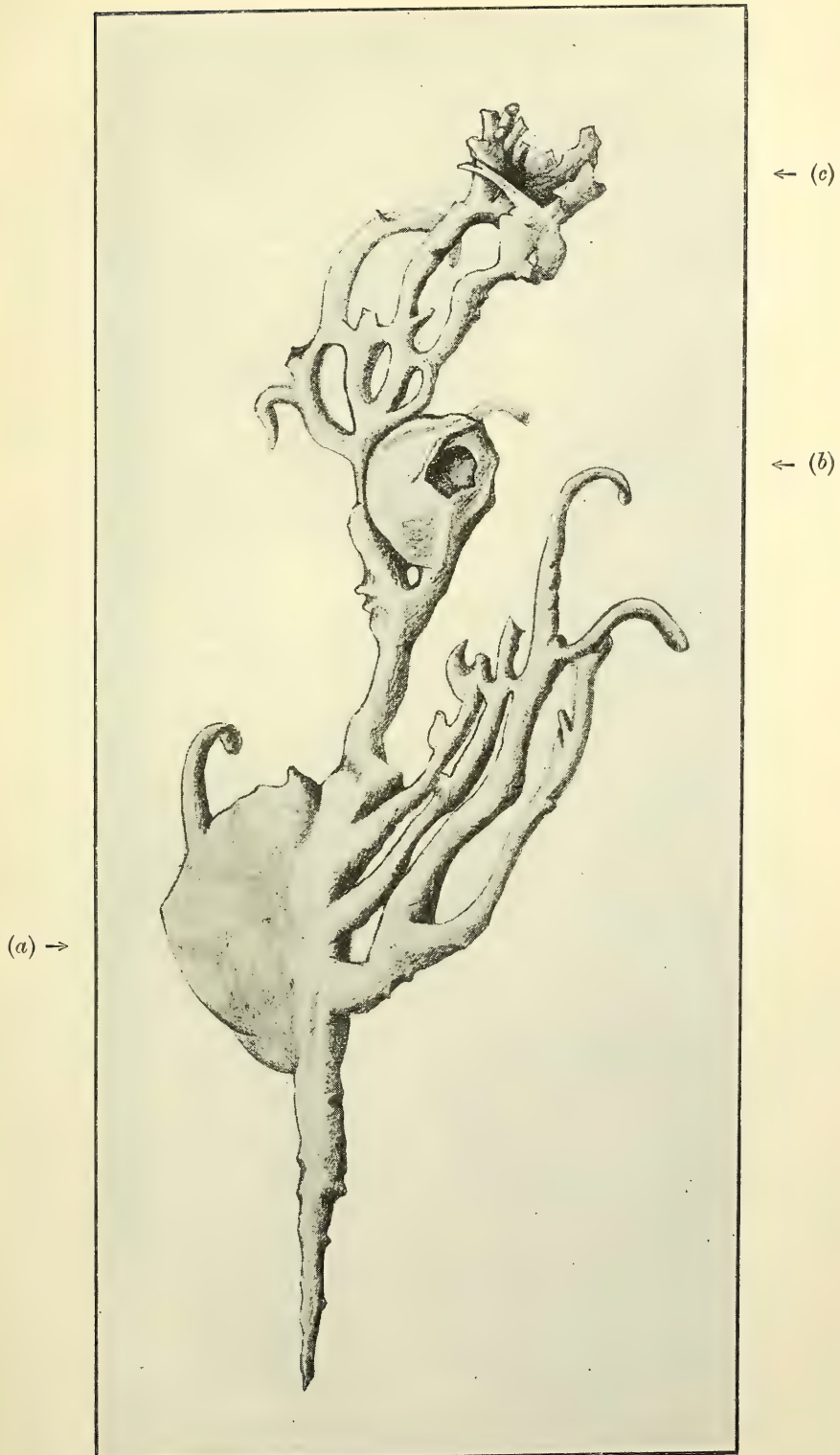
The imperfect gall at the top (*c*) is widely open, and is formed of a network of Millepore branches imperfectly woven together.

The extent of the malformation produced by these crabs need not be described as it is adequately represented in the illustration, but, I may add, the surface of the coral forming the outer wall of the gall shows no signs of unhealthiness or weakness. The cycles of pores are as numerous and as regular as in other parts of the corallum with normal growth, and the pores themselves are just as large and as well defined there as elsewhere.

These galls cannot, therefore, be regarded as a disease, although they effect a considerable alteration in the normal growth of the corallum.

NOTE.—The description of the gall-forming crab, given by Dr. Semper, and referred to above, is as follows:—"So long ago as the year 1837 Stimpson described a small crab, under the name of *Hapalocarcinus marsupialis*, which had been discovered in the Pacific Ocean by Dana, in the course of his great voyage under the command of Wilkes. Irrespective of other peculiarities this was distinguished from all other crabs by a remarkable pouch, in which the female carries the young, formed by a prolongation of the lateral plates of the abdomen."

The singular mode of life of these crabs, which was first observed by Semper, who studied them alive in the Philippine Islands, is thus described by him. For gall-forming crabs "an association," he says, "with living corals is indispensable, and the influence of the Corals on the Crabs is as direct and important as that of the Crabs on the Corals.



A. M. H. *del.*

CRAB-GALL ON MILLEPORA.

Hapalocarcinus has hitherto been detected only in pieces of branching corals of different genera On all these corals the crabs produce a peculiar excrescence on the twigs (so to speak) of a branch; these growths grow opposite each other in such a way that the crab settled between them is perfectly surrounded, and thus enclosed, in the gall which gradually forms A diseased¹ excrescence is first produced by the young crab establishing itself between the two branches, and the twig thus originating takes various forms according to the character of the species of coral In the first instance the two leaf-like twigs are, of course, far apart, so that the crab could easily get in and out; but as it does not do this, it is soon so surrounded by the growing together of the twigs that it must remain a prisoner. The creature requires a constant and rapid renewal of the water in the gall in which it lives for respiration Since in all the crabs of this group the current of water for breathing enters the body close to the mouth, and passes out again at the hinder margin of the branchial [respiratory] cavity, the stream passing through the gall must always flow in one and the same direction The two excrescences on the coral grow together quickest in those spots which are least exposed to the current through the gall at length only two fissures are left, which plainly show that it is through them that the current for respiration passes These two slits remain open so long as the crab is alive; no living crab is ever found in a closed gall, and they are for the most part perfectly empty."

¹ The excrescences show, as stated above, no signs of disease.

From the "PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON,"
January 17, 1899.

REPORT ON THE GORGONACEAN CORALS COLLECTED BY
MR. J. STANLEY GARDINER AT FUNAFUTI.

By ISA L. HILES, B.Sc. (Vict.), *Owens College, Manchester.*

Plates XII.—XV.

Of the forms of Gorgonacean Corals sent to me by Mr. Gardiner for identification and examination the majority belong to the family Muriceidæ.

There is one Gorgonellid—*Verrucella granifera* Kölliker; two Sclerogorgic forms of Gorgonidæ—*Suberogorgia verriculata* Esper, and *Kerceides koreni* Wright and Studer; and one Plexaurid *Euplexaura antipathes* Klunzinger.

Among the representatives of the Muriceidæ there are three new forms—*Villogorgia rubra*, *Acamptogorgia spinosa*, and *Muricella flexilis*.

The specimens have been very carefully preserved in spirit, but unfortunately in some cases the endoderm is not complete, and therefore they are not so useful for anatomical examination as they would otherwise be.

I am much indebted to Professor Hickson for the great help he has given me, especially with regard to the literature. The classification adopted is that used by Wright and Studer in the 'Challenger' Report on Aleyonaria.

Section SCLERAXONIA.

Family SCLEROGORGIDÆ.

KERCEIDES KORENI Wright and Studer.

There are numerous fragments of this species, but no complete colony.

The spicules are .92 mm.--203 mm. in length, by .27 mm.--.13 mm.

The colony is light red in colour, with yellow polyps.

Hab. Outer slope of the reef. Depth 40-90 fathoms.

Previously recorded from the neighbourhood of Japan (7),

Section HOLAXONIA.

Family MURICEIDÆ.

ACAMPTOGORGIA SPINOSA, n. sp. (Plate XII., Figs. 3, 4, 5).

There are several fragments of this form, but they are all rather small.

The branches are .5 mm. in diameter. The cœenchyma is fairly thick and very rough. The small branches arise at angles of from 60°-90°. The polyps are borne chiefly on the sides of the branches. They stand out fairly perpendicularly at intervals of about 2 mm.

Each branch bears, close to the apex, two opposite polyps which are usually somewhat larger than the others. They are 1.05 mm. in height, by 1.1 mm. across the crown and .64 mm. across the base.

The other polyps are .73 mm. × .62 mm., and .55 mm. across the base. Thus the terminal polyps are decidedly larger than the lateral ones. They are cylindrical in shape, somewhat wider across the crown.

The operculum forms a low cone; it consists of the basal spicules of the tentacles, each tentacle having 2 or 3 long-pointed spicules which divide into two at the basal end. They are .36 mm. × .09 mm. (length by breadth), and rest on a sunken collaret of spindles.

The polyp spicules are of the three-rayed type, with foliaceous expansions from two of the three rays, the third standing perpendicular to the others like a long sharp spike. They are .37 mm. in height by .36 mm. across the foliaceous basal portion.

The cœenchyma spicules are bent spindles with short branched expansions on the convex side, and also smaller forms of the polyp spicules. The spindles are .21 mm. × .11 mm. (length by breadth).

The axis is horny, brown, with the central core divided into chambers

The colour of the colony in spirit is light brown.

Depth 40-90 fathoms.

This form differs from *A. arbuscula*, *A. alternans* Wright & Studer, *A. acanthostoma* and *A. fruticosa* Germanos, in the structure of the polyps, their proportionate size to the width of the branch, and the shapes of the spicules. The spicules resemble most closely those of *A. acanthostoma*, but the polyps of the new species are much more spiny.

ACANTHOGORGIA MURICATA Verrill. (Plate XII. Figs. 6, 7.)

Verrill (4) gives no figures, but the specimen agrees fairly with his description of the species.

The branching is in one plane.

Height of the specimen 75 mm.; breadth 8 mm.; diameter at the base 1 mm.

Length of the calyces 2.0-2.5 mm.; diameter at the base .6 mm.; diameter of the head 1.2 mm.

The spicules round the edge of the calyx are $1.01 \times .06$ mm.; the spicules of the calyx-wall are $.75 \times .03$ mm.; the spicules of the cœnenchyma are $.3 \times .03$ mm. Most of the spicules are crooked, and some have the smaller end slightly branched.

Depth 40-90 fathoms.

Previously recorded from Barbados. Depth 76 fathoms.

This is a good example of wide distribution, the same species being found at Barbados and at Funafuti, two widely separated localities.

VILLOGORGIA INTRICATA Gray.

There is one example of this species attached to the axis of a dead Gorgonid. Wright and Studer (7) describe the species among the 'Challenger' Gorgonidæ.

Depth 40-71 fathoms.

Previously recorded from a locality between the Fiji Islands and the New Hebrides. Depth 145 fathoms.

This is a considerable difference in depth, but the specimen is undoubtedly *V. intricata*.

VILLOGORGIA RUBRA, n. sp. (Plate XIII. Figs. 1, 2, 3, 4.)

There are two small colonies with much of the cœnenchyma rubbed off.

The basal attachment is present in both as a small, flat, calcareous expansion.

One colony gives off a broken branch at an angle of 90° , 10 mm. above the base; the main stem reaches a height of 40 mm., and 13 mm. from the apex gives off another branch at the same side, 8 mm. long.

The other colony is 34 mm. high and gives off three branches fairly perpendicularly. These are all on the same side; the lowest arises 11 mm. from the base and is broken off short; the second is 9 mm. long, and arises 3 mm. above the first; the third is 4.5 mm. above the second, and is 13 mm. long.

There are very few polyps, most of the cœnenchyma having been rubbed off; but what remains of the cœnenchyma is thin. The polyps arise almost perpendicularly, and mostly on the two sides. The end of a branch bears two polyps, only slightly in advance of the other, but neither truly terminal. The polyps are .92 mm. in height by 1.3 mm. in breadth at the base.

The spicules of the cœnenchyma are chiefly four-rayed stars and flattened curved spindles, giving off spines from the convex side. They are .12 mm. long by .2 mm. broad.

The polyps are covered with broad flat spicules, somewhat triangular in shape, with branched lateral outgrowths. They are .22 mm. $\times$.49 mm. (length by breadth).

The operculum is eight-rayed; each ray consists of two broadish spicules, converging at the apex. Their bases rest on a horizontally placed spicule, curved in shape and somewhat spiny. The opercular spicules are .31 mm. $\times$.07 mm.

The axis is horny, flexible, with the centre divided into chambers.

The colour of the colony in spirit is reddish brown. The spicules of the cœnenchyma and polyps are bright red, those of the operculum white.

Hab. Outer slope of Ellice Island. Depth 40–71 fathoms.

This form differs from *V. intricata* Gray in the size of the polyps and of the spicules, the arrangement of the polyps, and the colour of the spicules.

It differs from *V. mauritiensis* Ridley (5) in the size of the polyps, the shape of the spicules of the verrucæ, and the colour of the colony.

It differs from *V. flabellata* Whitelegge (9) in the colour and form of the spicules.

It differs from *V. nigrescens* Duchassaing & Michelotti (1) in the form and size of the verrucæ and in the colour of the colony.

MURICELLA FLEXILIS, n. sp. (Plate XIV. Figs. 1, 2.)

There is one small specimen of this form. It is 130 mm. in height and 70 mm. across the widest part. The main stem is 1.5 mm. in diameter near the base.

Branching takes place in one plane, the branching arising from two sides of the stem. Lateral branches are borne in the same plane. The branches are slightly flattened in the plane of branching; they all end in a small flat expansion with two lateral polyps borne close to the apex, making it somewhat hammer-shaped.

The calyces are .9 mm. by .8 mm. in diameter at the base. The polyps are only partially retracted, the heads, measuring .6 mm. $\times$.5 mm. in diameter, being visible above the verrucæ.

The spicules are spindle-shaped, with warts not very thickly placed. They are 1.105 mm. $\times$.09 mm., .83 mm. $\times$.073 mm., .18 mm. $\times$.027 mm.

The colour in spirit is dirty white, the brown axis showing through the thin white cœenchyma.

Hab. Outer slope of the reef of Funafuti. Depth 40–71 fathoms.

This specimen differs from *M. tenera* Ridley (5) in the greater slenderness of stem and branches, the smaller size of the spicules, and the fact that they are much less warted.

It differs from *M. umbraticoides* Studer¹ in the absence of the "halbseitig warzig" character of the spicules.

It differs from *M. complanata* Wright & Studer (7) in its much more slender appearance, the thinness of the cœenchyma, and the comparatively smooth character of the spindles, and also in colour, being white, not rose colour.

It differs from *M. perramosa* Ridley (5) in colour and in the absence of a divergent bend of the stem at the origin of the branches.

It differs from *M. nitida* Verrill (4) in colour, in the size of the spicules, and the lateral position of the polyps.

It differs from *M. gracilis* Wright & Studer (7) in the lateral arrange-

¹ Studer, Th., Monatsber. d. k. Akad. d. Wiss. Berlin, 1878.

ment of the polyps at the ends of the branches, in the much less warted spindles, and in the colour of the coenenchyma, which is not red but white.

It differs from *M. crassa* Wright & Studer (7) in the thinness of the coenenchyma, the lateral arrangement of the polyps, the slender character of the stem and branches, and in the much smoother character of the spicules.

MURICELLA TENERA Ridley, (Plate XIV. figs. 3, 4.)

There is one colony; it is 115 mm. high by 55 mm. across the widest part. The main stem is 2 mm. in diameter at the base. It is ramified in one plane, giving off branches on two sides at angles of about 45°; these again bear branches at angles of 45°-60°.

The calyces are small and inconspicuous, .5 mm. high and 1 mm. in diameter at the base. They are borne on the two sides of the stem and branches about 2 mm. apart.

The branches end in two laterally placed polyps, making the termination triangular in shape.

The coenenchyma is thin and whitish in colour; the brown axis shows through, making the whole appear fawn-colour. The polyps are brown.

The spicules are long, wavy spindles, covered with warts, which are more prominent on one side than the other. They are 4.34 mm. × .29 mm., 2.34 mm. × .22 mm., .29 mm. × .036 mm.

Hab. Outer slope of the reef. Depth 40-71 fathoms. This specimen differs slightly from *Muricella tenera* as described by Ridley (5), but the differences are not very important. The calyces are smaller, and the spicules are from two to four times the size of those of Ridley's form.

The spicules of the calyx also are not arranged in such a regular row as Ridley figures; Wright and Studer (7. p. 124) say the same about these spicules in the forms examined by them.

Otherwise the colony decidedly approaches *M. tenera*: I have seen the 'Challenger' specimen, and consider this to be the same form.

Previously recorded from south of Papua, off the Ki Islands, depth 140 fathoms; and Port Molle, Queensland.

Family PLEXAURIDÆ.

EUPLEXAURA ANTIPATHES Klunzinger. (Plate XV. Figs. 1, 2.)

Plexaura antipathes Klunzinger.

This specimen which is in a dried state, is pale fawn in colour.

The colony is much branched, the branches arising approximately in one plane. The branches are given off irregularly; they, in their turn, branch repeatedly, and these branches bear further branches. There are no traces of anastomoses. The basal portions are slightly flattened, but the terminal twigs are round and thicken slightly towards the ends. The branches run close together and fairly parallel.

The polyp-pores are scattered irregularly over the whole surface, and are not raised above the general level except on the terminal twigs, where they are at the summit of slight conical elevations. They are about 1 mm. apart.

The cortex is friable, and somewhat thicker on the twigs than the older parts. It is comparatively smooth; on the older branches there are slight longitudinal furrows which run somewhat spirally round the stem. The axis is of horn, with scattered particles of calcareous matter; it is of a dense black colour in the thicker branches.

The "root" portion of the colony shows a great development of a peculiar skeletal substance, hard, and looking like stone. It is dull grey in colour, and shows the same furrowings as the cortex of the stem which extended over it. On treating with acid the stony part is dissolved away, leaving a fine network of horny matter in which the CaCO_3 was contained.

The grey substance which strengthens the base of attachment is clearly formed independently of the black axis, although it may rightly be regarded as being of the same nature. Judging from the dried specimen it is composed of spicules of lime embedded in a horny matrix, no processes of the cœnosarcæ extending into it, even superficially. It is extremely hard, and breaks with a clean fracture when struck with a hammer. The horny axis, on the other hand, can be cut with a pen-knife. The nature of the horny substance is not determined, but from its insolubility seems similar to the keratin of the axis. It is only rarely seen in specimens of Gorgonacea in Museums, although it is possible that it may be formed at the base of all large Gorgonids when exposed to strong tides.

In the centre the calcareous matter is white and friable, not having assumed the stony, solid appearance of the outer part.

The basal enlargement is seen also in *Plexaura principalis* and *P. suffruticosa*, in the National Collection at South Kensington; and Klunzinger, in his 'Korallthiere des Rothen Meeres,' mentions it for *Plexaura antipathes*.

The spicules of the cortex are small warty spindles and clubs, the spindles preponderating. They are colourless, and are $\cdot 17$ mm. in length by $\cdot 07$ mm. in breadth. There are also a few small irregular crosses.

Hab. Funafuti Lagoon. Depth 6-7 fathoms.

Family GORGONELLIDÆ.

VERRUCELLA GRANIFERA K  lliker. (Plate XII., Figs. 1, 2.)

Syn. *Verrucella flabellata* Whitelegge.

There are several fragments of this species. The largest is 170 mm. long; the stem is 1 mm. in diameter at the base, and remains about the same throughout. At a height of 70 mm. it gives off a branch, and 50 mm. farther another branch arises. The branches are about the same thickness as the stem. The whole is whip-like and very flexible.

The verruc  e are numerous, alternate, nearly at right angles to the axis, and about 2 mm. apart. They are $\cdot 5$ mm. high by 1 mm. wide at the base, and bluntly conical in shape.

The axis is very hard and brittle; it shows a number of longitudinal grooves.

The branches end in a small knob, with a laterally-placed polyp close to the apex. The spicules are double stars and spindles of the Gorgonellid type. The warts are compound, and arranged in rings, leaving a median zone free and smooth. The spindles are flat, and many of them have rounded ends. The double spindles are $\cdot 073$ mm. $\times$ $\cdot 036$ mm., $\cdot 082$ mm. $\times$ $\cdot 018$ mm.; the double stars are $\cdot 036$ mm. $\times$ $\cdot 018$ mm.

The colour, in spirit, is pale fawn.

These specimens seem to approach most closely to *Verrucella granifera* K  lliker (2), except that the spicules are only faintly tinged with yellow.

V. flabellata Whitelegge (9) seems to resemble K  lliker's form, *V. granifera*, very closely, the only difference, apparently, being that some of the spicules have rounded ends; but others, as he figures

(Pl. XVII. Fig. 33), have pointed ends, and resemble those of *V. granifera*. This seems a small difference on which to found a new species, especially when the character is not constant and found in all the spicules. In one of the pieces from Funafuti which I examined, the spicules are decidedly longer and more pointed than in the other fragments although in other respects they are similar. This may be due simply to a difference in locality. A slight variety of form and size in the spicules is of frequent occurrence in Gorgonacea, and must not be considered of specific value.

Hab. Funafuti. Depth 40-71 fathoms. Previously recorded from the coast of Africa.

This is another instance of the same species from two widely separated localities, and may be compared with the distribution of *Acanthogorgia muricata* Verrill, which occurs at Funafuti and has been recorded from Barbados.

SUBEROGORGIA VERRICULATA Esper.

There are two fragments of this species, drab in colour.

The double star spindles are somewhat rougher than those figured in Kölliker's paper (2), otherwise the form seems to belong to Esper's species.

Hab. Outer slope of the coral-reef at Funafuti.

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EXPLANATION OF THE PLATES.

PLATE XII.

- Fig. 1. *Verrucella granifera*, p. 158. A branch, natural size.
2. *Verrucella granifera*. Some spicules.
3. *Acamptogorgia spinosa*, n. sp., p. 152. A small portion of a branch, magnified, to show the arrangement of the spicules.
4. *Acamptogorgia spinosa*. The crown of a polyp, magnified, to show the arrangement of the opercular spicules.
5. *Acamptogorgia spinosa*. Some spicules, (a) of the operculum, (b) of the cœnenchyma.
6. *Acanthogorgia muricata*, p. 153. A polyp, magnified.
7. *Acanthogorgia muricata*. Some spicules, (a) of the operculum, (b) of the cœnenchyma, (c) of the polyp.

PLATE XIII.

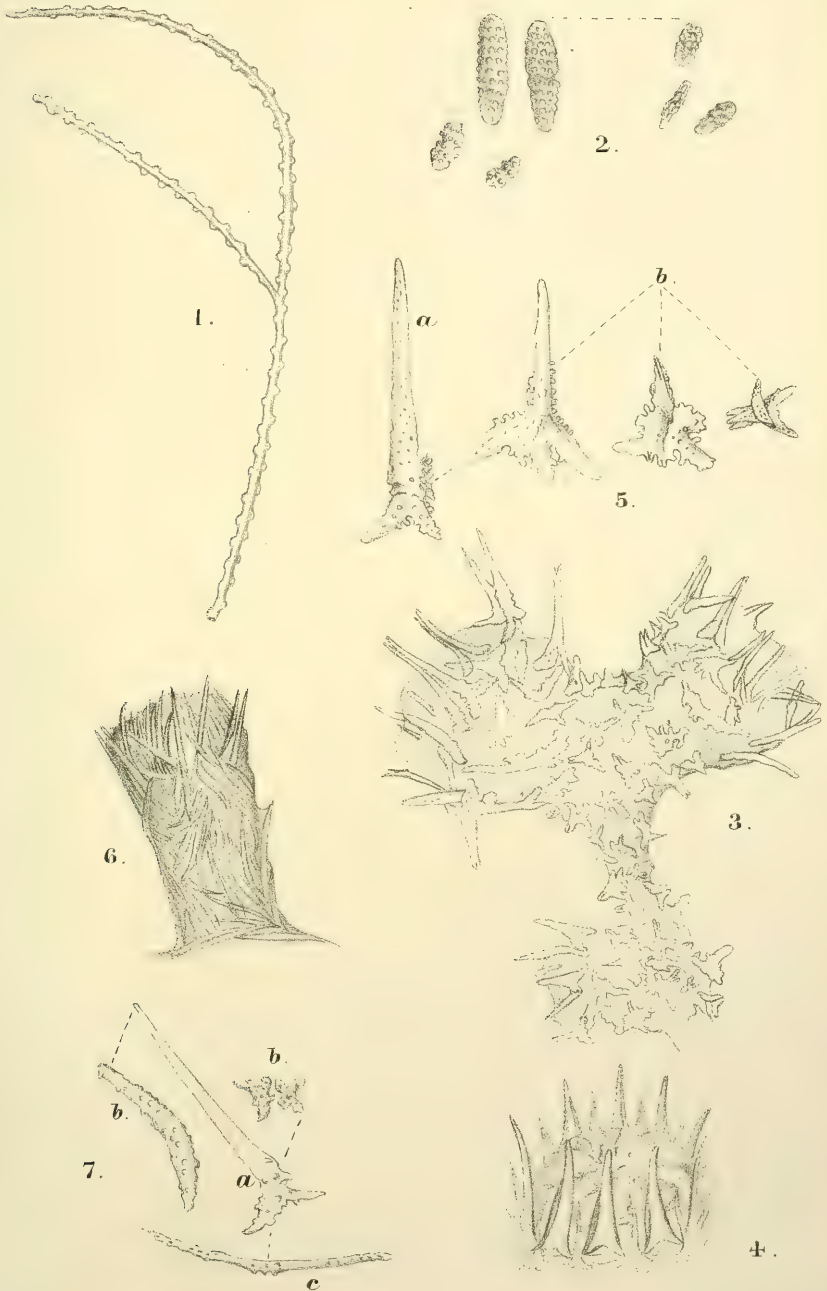
- Fig. 1. *Villogorgia rubra*, n. sp., p. 153. The colony, natural size.
2. *Villogorgia rubra*. Some spicules, (a) of the operculum, (b) of the polyp, (c) of the cœnenchyma.
3. *Villogorgia rubra*. Three polyps, magnified, to show the operculum closed.
4. *Villogorgia rubra*. Two rays of the operculum.

PLATE XIV.

- Fig. 1. *Muricella flexilis*, n. sp., p. 155. The colony, natural size.
2. *Muricella flexilis*. Some spicules.
3. *Muricella tenera*, p. 156. The colony, natural size.
4. *Muricella tenera*. Some spicules.

PLATE XV.

- Fig. 1. *Euplexaura antipathes*, p. 157. The lower part of the colony, $\times \frac{1}{2}$, to show the stony basal enlargement.
2. *Euplexaura antipathes*. A small portion of a microscopical section of the basal part, decalcified, showing the horny matrix.



J. Smit lith.

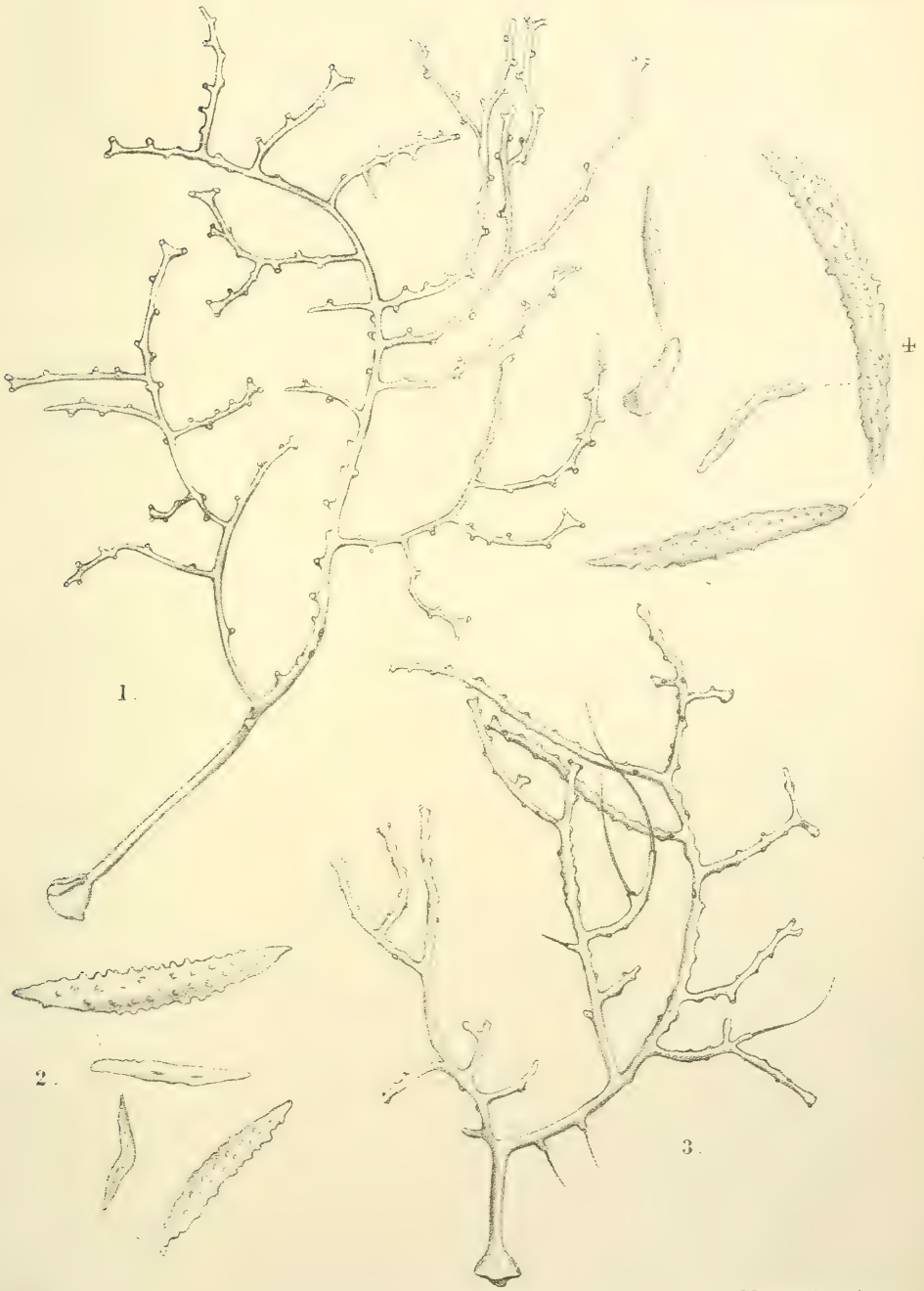
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FIGS. 1, 2. *VERRUCELLA GRANIFERA*. FIGS. 3-5. *ACAMPTOGORGIA SPINOSA*.
FIGS. 6, 7. *ACANTHOGORGIA MURICATA*.









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Figs. 1, 2 MURICELLA FLEXILIS.

Figs. 3, 4 M. TENERA.





Reprinted from the "BERICHTE DER DEUTSCHEN BOT. GESELLSCHAFT,"
Jahrgang, 1899. Band XVII., Heft 1.

CHANTRANSIA ENDOZOICA DARBISH, EINE NEUE
FLORIDEEN-ART.

By O. V. DARBISHIRE. Eingegangen am 16 Januar, 1899.

Mit Tafel XVI.

Die im Folgenden als neu beschriebene Art wurde mir zur Bestimmung von Herrn Prof. F. E. Weiss übergeben, der das Material bei Valencia an der Südküste von Irland gesammelt hatte. Durch die Freundlichkeit der Herren E. A. L. Batters und Dr. P. Kuckuck wurde ich in die Lage versetzt, die unserer neuen Art verwandtschaftlich am nächsten stehenden Chantransien an conservirtem Material selbst untersuchen zu können. Dafür sage ich diesen Herren hiermit meinen besten Dank.

Chantransia endozoica Darbish. wuchert in der äusseren Wandung und auch im Innern von *Alcyonidium gelatinosum* L., eines marinen thierischen Organismus, der durch die Gegenwart des Gastes ein ganz rothes Aussehen bekommt und etwa folgenden Aufbau aufzuweisen hat. Eine Anzahl Individuen bilden einen zusammenhängenden Stock, der durch eine gemeinsame, feste Schicht nach aussen begrenzt ist. In grosser Anzahl stehen auf dieser Aussenwand kleine conische Höcker, deren äussere Schicht mit der des übrigen Stockes fortlaufend ist. Der conische Höcker ist nur eine Ausstülpung der gewöhnlichen Wandung des Stockes. Es befindet sich in demselben ein Hohlraum, der auch nach dem Innern des Stockes zu durch eine Wand begrenzt ist. Auch das Innere des ganzen Stockes scheint durch Wände mehr oder weniger gekammert zu sein. Diese Wände sind fast von derselben Dicke, wie die Aussenwände des ganzen Stockes. Zwischen den conischen Höckern finden sich Oeffnungen in der Aussenwand, welche in das Innere des Thierstockes führen. In dem unter

dieser Oeffnung liegenden Hohlraum befindet sich einer der vielen Polypen, welche den lebenden Theil des Gesamtorganismus ausmachen. *Alcyonidium* gehört zu der Klasse der Bryozoen.

Diese kurze Beschreibung der Unterlage, welche *Chantransia endozoica* Darbish. bewohnt, wird genügen, um die Lebensweise dieser kleinen Floridee im Folgenden klarlegen zu können.

Chantransia endozoica Darbish. kommt zuerst nur in der äusseren Wandung des Thierstockes von *Alcyonidium gelatinosum* L. vor. Sie durchwuchert diesen Theil nach allen Seiten und dringt sogar schliesslich in den lebenden Theil des Thierstockes ein, ja befällt in einigen Fällen selbst die in demselben befindlichen Polypen. Es muss hier bemerkt werden, dass bei dem untersuchten Material scheinbar nur ein Theil der Polypen in völlig gesundem Zustande war, in Fällen, wo die Thiercolonie von *Chantransia endozoica* Darbish. befallen war.

In dem Innern des thierischen Substrates und in den Wandungen desselben wuchert nur der rein vegetative Theil der Alge, die fort-pflanzenden Thallusabschnitte entwickeln sich ausserhalb des Wirthes (Tafel XVI., Fig. 1).

Die vegetativen Fäden sind reichlich gabelig verzweigt. An Stellen, wo ein intensives Wachstum stattzufinden scheint, sind die Zellen meist ziemlich lang gestreckt, während sie an Stellen, wo das Wachstum wegen Raummangels im Begriffe ist nachzulassen oder ganz aufzuhören, kürzer und breiter sind. Die letzteren findet man am zahlreichsten und am dichtesten in den schon mehrfach erwähnten conischen Ausstülpungen, die ersteren mehr in dem inneren Gewebe des Thierstockes.

In dem conischen Anwuchse bilden die Fäden des Gastes allmählich ein ziemlich dichtes Gewebe, das die Wandung bald fast ganz ausfüllt. Normalerweise scheint diese Wandung etwa 5—6 μ dick zu sein, durch das Wuchern unserer kleinen rothen Alge steigt ihre Dicke auf 17—20 μ .

Die vegetativen Zellen in den conischen Ausstülpungen sind 6,8—8,5 μ lang und bis 5 μ breit. Zwischen diesen längeren Zellen finden sich viele, meist ältere Zellen, welche von ziemlich runder Gestalt sind und 6,8—8,5 μ nach jeder Richtung messen. Daneben finden sich einige, die sehr schlank und bis 20 μ lang sind. Diese scheinen meist nach dem Innern des Thierstockes hinzuwachsen.

Die Auszweigungen des vegetativen Thallus im Innern von *Aleyonidium* bestehen in der Regel aus langen, schmalen, äusserst dünnwandigen Zellen, die 17—25 zu 2,5—13,6 μ messen. Dazwischen finden sich kürzere von 5,1—13,6 μ Grösse. Hier im Innern ist die regelmässige, gabelige Theilung am besten zu sehen (Tafel XVI., Fig. 2).

An einigen Stellen dringen diese Fäden bis zu einer Tiefe von 1 mm in das Innere des Thierstockes. Unsere *Chantransia* erreicht hier also eine ganz beträchtliche Länge.

Die ganze äussere, lederartige Wandung des Thierstockes kann mit diesen Fäden durchwuchert sein, indem von dem *Chantransia*-Pflänzchen eines conischen Auswuchses Fäden in die benachbarten Höcker übergehen. Die trennende Strecke legen die Ausläufer in der tiefer liegenden Wandung zurück (Tafel XVI., Fig. 1, bei b).

Zahlreich entsteigen den flach verlaufenden vegetativen Fäden aufrechte Aeste, welche die äussere Wandung durchbrechen und dann in's Freie hinausragen. Es sind dies die fertilen Aestchen, welche eine Höhe von 85 μ erreichen können. Ihre Zellen messen, 6,8 bis 8,5 μ zu 10—15 μ . Auch hier findet nur eine einfache gabelige Theilung statt. Bis jetzt ist es mir nur gelungen, die Bildung von Fortpflanzungsorganen zu beobachten, die ich für Monosporen halte. Sie kommen reichlich zur Ausbildung und messen bei etwa eiförmiger Gestalt $12 \times 10 \mu$ im Durchmesser. Ist ein Monosporangium entleert, so dringt von den darunter sich befindlichen, das Sporangium tragenden Zellen von Neuem das Plasma in die alte Hülle des Sporangiums, mit einer neuen Membran umgeben. In älteren Exemplaren sieht man oft drei Membranen ausserhalb der jüngsten Membran. Möglicherweise liegen hier nicht Monosporangien, sondern Spermatangien vor. Das Material war in Spiritus conservirt, so dass die rothe Farbe nicht mehr zu sehen war. Weitere Fortpflanzungsorgane wurden nicht beobachtet.

Die fertilen Aestchen entstehen sehr zahlreich auf der Wandung des ganzen Thierstockes. Am häufigsten scheinen sie jedoch auf den conischen Auswüchsen zur Ausbildung zu kommen.

Nicht selten ist die basale Zelle des fertilen Aestchens besonders ausgebildet. Sie ist dann ziemlich gross, von fast gleichmässigem Durchmesser nach allen Richtungen und meist mit einer dickeren Membran versehen, als die übrigen Zellen des vegetativen Thallus.

Die dickere Wand kennzeichnet auch die anderen Zellen des fertilen Aestchens. Die Membran wird bis $1,5\ \mu$ dick. Die basale Zelle sitzt meist noch in dem Substrat (Tafel XVI., Fig. 1, bei a).

Allmählich bildet sich in den älteren Theilen von *Alcyonidium gelatinosum* L. in den conischen Ausstülpungen eine fast pseudo-parenchymatische Zellplatte aus, die nicht selten bis zu zwei Zellen tief ist. Der ursprünglich fädige Charakter des Thallus von *Chantransia endozoica* Darbish. lässt sich dann meist nicht mehr erkennen.

Nur einmal schien eine Endzelle in ein Haar auszulaufen, doch kann dieses irgend einem fremden Organismus angehört haben. In Gestalt von kleineren Algen und Bakterien u. s. w. bedeckten an solchen älteren Theilen von *Alcyonidium* die verschiedensten Organismen in dichten Rasen den Thierstock. Ein Ursprung des Haares von dem nächsten *Chantransia*-Pflänzchen war nicht festzustellen.

Für die eben beschriebene neue Art möchte ich folgende kurze Diagnose geben :

CHANTRANSIA ENDOZOICA DARBISH. NOV. SP.

Der Thallus, reichlich gabelig verzweigt, wuchert in der äusseren Wandung des marinen Thierstockes von *Alcyonidium gelatinosum* L. kann aber an Stellen bis zu 1 mm tief in denselben eindringen. Vornehmlich lebt der Gast in den conischen Auswüchsen der Oberfläche des Wirthes, von wo aus sich Fäden in die benachbarten Theile des letzteren ausbreiten. Die vegetativen Zellen sind $6,8$ bis $25\ \mu$ zu $6,8$ bis $13\ \mu$ gross. Zahlreich entstehen senkrecht abstehende fertile Aestchen, welche die Wandung des *Alcyonidium* durchbrechen und so in's Freie gelangen und hier Monosporangien (oder Spermatangien?) bilden. Die fertilen Aestchen werden bis zu $85\ \mu$ hoch und sind nur wenig verzweigt. Die Fortpflanzungszellen sind von etwa eiförmiger Gestalt und messen $12 \times 10\ \mu$. Haarförmige Gebilde sind nicht mit Bestimmtheit beobachtet worden.

Bei Valencia an der Südwestküste von Irland gefunden (F. E. WEISS).

UEBER EINIGE NAHE VERWANDTE ARTEN VON CHANTRANSIA.

Chantransia microscopica (Nägeli) Batters (1, S. 3) und die hierzu gehörigen Varietäten *pygmaea* Kuckuck (4, S. 391) und *collopoda* Rosenvinge (3, S. 41) sind unserer *Chantransia endozoica* Darbish. nicht unähnlich. Die erste Varietät wuchert in dem Thallus von *Porphyra*

laciniata (Lightft.) C. Ag. Dem einfachen Bau der Wirthspflanze entsprechend hat auch der Eindringling einen sehr einfachen Aufbau aufzuweisen. Er erreicht keine grossen Dimensionen. Nach KUCKUCK sind die vegetativen Zellen seiner neuen Varietät 3 bis $3,4 \mu$ breit, bei der BATTERS'schen Art 4,5 bis 7μ breit, während KOLDERUP-ROSENVINGE für seine Varietät *collopoda* die Breite der vegetativen Zellen als 7 bis 8μ , die Länge als 12 bis 28μ angiebt. Diese Varietät kommt auf *Chordaria flagelliformis* (Müll.) Ag. vor. Sie besitzt ein grosses Basalorgan.

Bei unserer Art fehlt die *Chantransia microscopica* (Näg.) Batters und varr. kennzeichnende Bildung eines Basalorganes. Angedeutet findet sich das letztere bei *Chantransia endozoica* Darbish., indem man gelegentlich, wenn auch selten, eine etwas grössere basale Zelle am Grunde der fertilen Aestchen findet, die sich auch durch eine dickere Wandung auszeichnet.

Bezeichnend für unsere Art ist kurz das Fehlen von farblosen Haargebilden, sowie eines deutlich ausgeprägten Basalorgans.

Chantransia microscopica (Näg.) Batters befällt mit seinen Varietäten nur Algen, während *Chantransia endozoica* Darbish. in einem thierischen Organismus, *Alcyonidium gelatinosum* L., vorkommt. Für eine Floridee ist dieser Umstand von grossem Interesse. LAGERHEIM hat (6) eine Anzahl epizoischer Algen aufgeführt, und auch die perforirenden Algen wären vielleicht hierzu zu zählen, obgleich diese meist nur auf alten Schalen vorkommen. Von diesen ist die Floridee *Conchocoelis* Batters auch nur wenig bekannt. In gleicher Weise wie unsere neue *Chantransia* befällt auch die Chlorophyceen *Epicladia Flustrae* Rke. var. *Phillipsii* Batters (2, S. 2) und die Phaeophyceen *Endodictyon infestans* Gran (3, S. 47) Arten von *Alcyonidium*.

Neben der eben beschriebenen neuen Art bemerkte ich noch auf der Aussenseite von *Alcyonidium* Arten von *Delesseria*, *Polysiphonia*, *Erythrotrichia*, *Chylocladia*, *Plocamium* u. a. m., in Anfangsstadien. Oeffters wurden auch gekeimte und ungekeimte Sporen von rothen Algen ebendasselbst beobachtet, die zum Theil wahrscheinlich zu *Chantransia endozoica* Darbish. gehörten. Es ist mir nicht gelungen, festzustellen, auf welche Art und Weise diese Alge in das Wirthsthier eindringt.

Manchester, Owens College,

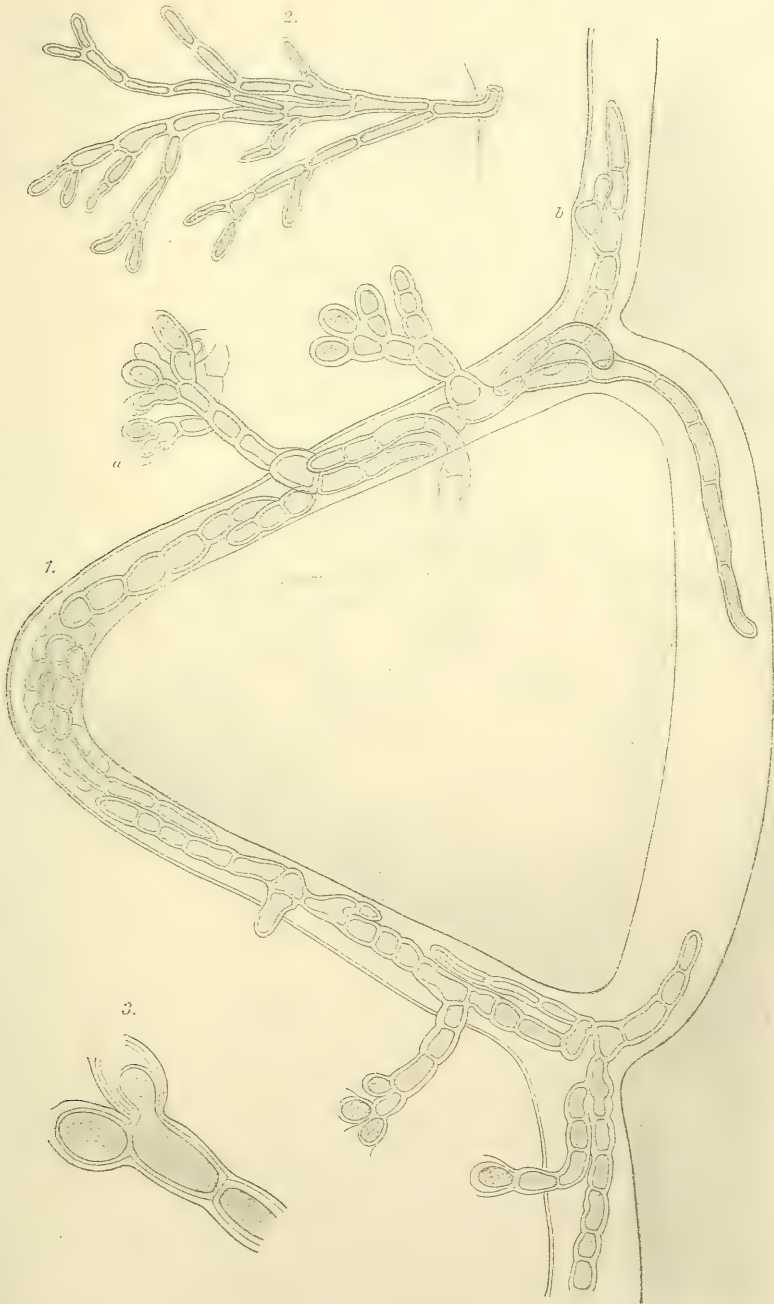
Januar 1899.

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ERKLÄRUNG DER ABBILDUNGEN.

- Fig. 1. Habitusbild eines ganzen Pflänzchens, wie es in einer conischen Ausstülpung der äusseren Wandung von *Alcyonidium gelatinosum* L. wuchert. Man sieht auch, wie mehrere Fäden mehr nach der Mitte des ganzen Thierstockes vordringen. Bei *a* ist ein kleines, fertiles Aestchen in voller Entwicklung ausserhalb des Substrates. Bei *b* ist ein Faden im Begriff die äussere Umwandung zu durchbrechen. Die zwei rechten fertilen Aestchen besitzen beide deutliche Basalzellen. Vergr. 400.
- „ 2. Einige langzellige Fäden ganz aus dem Innern des Thierstockes von *Alcyonidium gelatinosum* L. Vergr. 400. /
- „ 3. Endstück eines fertilen Astes mit zwei Monosporangien (oder Spermatangien?). Vergr. 800.



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ON ACTINOCOCCUS AND PHYLLOPHORA.

By OTTO VERNON DARBISHIRE, *The Owens College, Manchester.*

With Plate XVII. and seven Figures in the Text.

Credidi enim et etiamnunc credo, tubercula illa nihil aliud esse quam parasiticum quid . . .—LYNGBYE, *Tentamen Hydrophyt.* Dan., 1819, p. 11.

In 1893 Schmitz published a paper, in which he discussed at some length the *Actinococcus* question. He maintained that all so-called forms of fructification of *Phyllophora Brodiaei* (Turn.) J. Ag. which he had so far been able to examine, belonged in reality to a different Floridea growing parasitically on the former species (5, p. 371). This paper was shortly after reviewed by Gomont, who expressed his full agreement with the views held by Schmitz; so that the true nemathecium of *Phyll. Brodiaei* (Turn.) J. Ag. still remained to be found.

Doubts had long been felt with regard to the true nature of the so-called nemathecium of *Phyll. Brodiaei* (Turn.) J. Ag. The few lines quoted at the head of this paper were written by Lyngbye in 1819 in describing these very same nemathecium. In the beginning of 1894 the author of this paper gave a preliminary account of some observations on the anatomy and development of the Baltic species of *Phyllophora* Grev., in which Schmitz' assertions concerning the parasitic nature of the nemathecium of *Phyll. Brodiaei* (Turn.) J. Ag. were discussed and the accuracy of his conclusions was doubted (1, p. 47). A more detailed account of the author's work on the Baltic *Phyllophorae* was published about a year later, but unfortunately Schmitz died in 1894. In the

second paper just mentioned the author again expressed it as his opinion that the so-called nemathecium of *Phyll. Brodiaei* did really represent the true tetrasporic fructification of this Floridea (2, pp. 2 sq., 23 sq., 36).

The subject has not been worked at by algologists since, and Schmitz' theory has therefore naturally been most generally accepted. Kolderup Rosenvinge alone seems to have adopted an opposite view (4, p. 33).

Since commencing work on the anatomy and development of *Phyllophora* in 1892, the author has devoted much time to the examination of all forms of fructification found on it. Up to 1896 opportunity was however wanting for dredging and examining fresh material during the months of September and October, owing to the author's absence from Kiel during that time. Practically all the material used in these investigations was collected in the Baltic near Kiel. The observations carried out up to this point indicated that the one conclusion to be drawn was that the so-called (*Actinococcus*) nemathecium of *Phyll. Brodiaei* was really the genuine tetrasporic fructification of that plant.

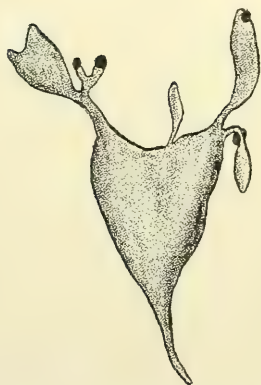


Fig. 1. Nemathecium of *Actinococcus roseus* (Lyngb.). Kold. Rosenv. on *Phyllophora Brodiaei* (Turn.) J. Ag. Nat. size.

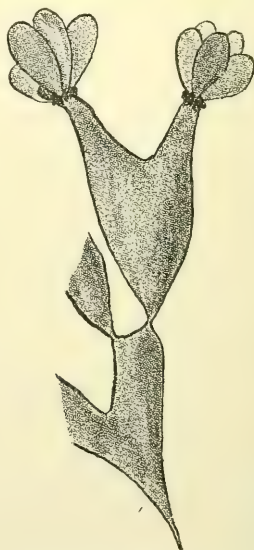


Fig. 2. Nemathecium of *Actinococcus roseus* (Lyngb.). Kold. Rosenv. on *Phyllophora Brodiaei* (Turn.) J. Ag. Nat. size.

In 1896 for the first time specimens of *Phyll. Brodiaei* were dredged and preserved at all times of the year. This was continued up to

September, 1898, when the author left Kiel. The development of the plant in question was followed out, and as a result the author has accepted Schmitz' view of the parasitic nature of *Actinococcus*, the correctness of which view, however, Schmitz unfortunately was not able to establish, as he did not succeed in observing the entrance of the parasite into the host.

The following is an account of the anatomy and development of *Actinococcus subcutaneus* (Lyngb.) K. Rosenv., which forms the 'pseudonemathecium' of *Phyll. Brodiaei* (Turn.) J. Ag.

ACTINOCOCCUS SUBCUTANEUS (Lyngb.) K. Rosenv.

Almost at every time of the year small, more or less spherical, dark reddish bodies are found on the flat expansions forming the thallus of

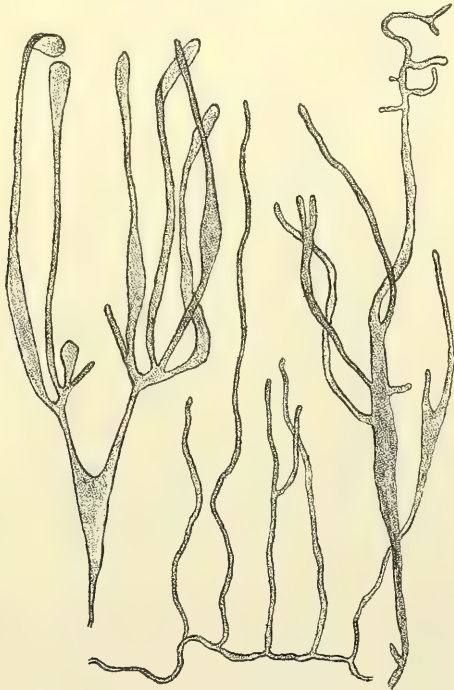


Fig. 3. *Phyllophora Brodiaei* (Turn.) J. Ag,
Sterile, Baltic forms. Nat. size.

Phyll. Brodiaei. They are sessile on the young shoots at the apex of

the thallus, but often appear to be stalked, this appearance being produced by the shoots on which they grow (Figs. 1 and 2) being at first rather narrow.

These red bodies are the nemathecium of *Actinococcus subcutaneus* (Lyngb.) Kolderup Rosenvinge, the Floridea mentioned above as growing parasitically on *Phyll. Brodiaei*. The young shoots of the latter Alga are not usually much modified by the presence of the parasite, but are on the contrary as a rule well developed.

In the Baltic sea small detached portions of the thallus of *Phyll. Brodiaei* frequently occur lying on the sea-bottom. They are

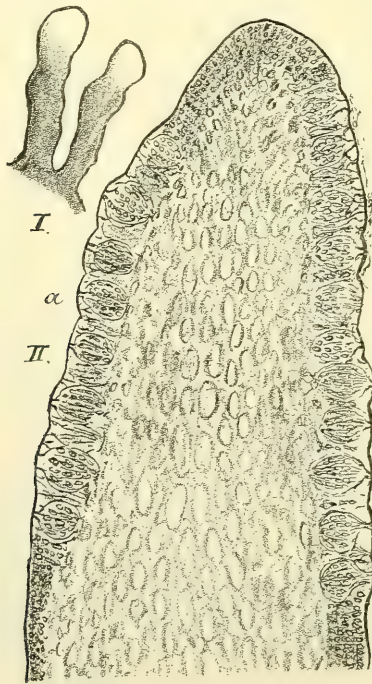


Fig. 4. *Phyllophora Brodiaei* (Turn.) J. Ag. I. Two spermophores. $\times 10$ diam. II. Longitudinal section of spermophore, showing the antheridial cavities in the cortical layer. $\times 200$ diam.

characterized by being very narrow, elongated and always sterile (Fig. 3, *forma, ligulata, elongata, &c.*, of various authors). They therefore never develop antheridia or procarpia. Furthermore they are never attacked, at any rate not successfully attacked, by the

germinating spores of *Actinococcus subcutaneus*. This parasite can only enter the host when the male (or the female?) organs of the latter are present. It has been known to the author for some time that the antheridial cavities of *Phyll. Brodiaei* often accompanied the presence of *Actinococcus subcutaneus*, but only during the last year has it become possible to explain definitely the significance of this appearance.

As the presence of the antheridial cavities is so intimately associated with the relationship of the two red Algae which form the subject of this paper, it might be useful to recall the structure of the former (2, p. 29).

The antheridia of *Phyll. Brodiaei* are developed in the cortical layer of the spermophores, the latter being shoots more or less modified temporarily for the production of the male organs (Figs. 4, 5). They are slightly flattened near the lighter coloured apex, attaining a length of about 3 mm., being rarely broader than 0.5 mm., and they are borne on the apical margin of the flattened vegetative thallus. In the cortex of such a spermophore, close to its apex and not further down from it than 1.0—1.5 mm., we find the small cavities which contain the antheridia. These cavities are flask-shaped and communicate with the exterior by a small ostiole. Their height is 24—34 μ , their breadth about 20 μ . From the flat bottom of the flask-shaped cavity arise a number of 2, 3, or even 4-celled antheridia, which produce the single male cells or spermatia, at their apex (Fig. 5). The spermatia pass out of the cavity through the ostioles, which measure about 6—10 μ across.

It is not necessary to describe the carpophores of *Phyll. Brodiaei*, on which the female organs are borne (vid. 2, p. 32, Figs. 46, 47). I have not been able to ascertain definitely whether our *Actinococcus* can enter its host by means of the opening caused by the projecting trichogyne. Very probably it does, as I have seen *Actinococcus*-bearing shoots of *Phyllophora*, in the cortical layers of which could be seen what were apparently remains of undeveloped carpogones. Antheridia and procarpia, moreover, do not occur on the same plant.

In the autumn it is possible to observe the entrance of *Actinococcus* into *Phyll. Brodiaei* by the small ostioles of the antheridial cavities. The spores (tetraspores or carpospores) which ultimately give rise to the nemathecium of *Actinococcus subcutaneus* germinate on the surface of the host about this time.

The immediate product of germination seems to be a small heap of perhaps 4—8 cells, one of which always comes to be near an ostiole leading to an antheridial cavity. The antheridial cavities are developed in large numbers and very close together (Fig. 4, II.). A filament is then formed, which passes into the host-plant through the antheridial ostiole (Plate XVII., Fig. 1).

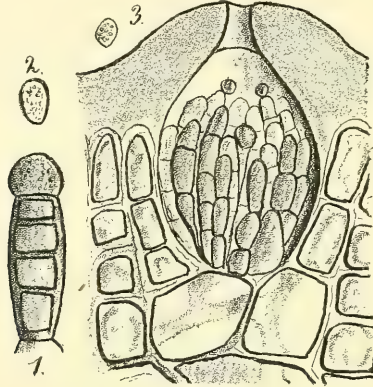


Fig. 5. *Phyllophora Brodiaei* (Turn.) J. Ag. 1. 4-celled antheridium with a spermatium at its apex. 2. Single spermatium. 3. Antheridial cavity with ostiole at its apex. $\times 1,000$ diam.

It is worth while perhaps to draw attention to a former figure which was intended to show the origin of the nemathecium of *Phyll. Brodiaei* (2, Fig. 31). It shows the nemathecium arising from the lower cells of the cortex or the outer cells of the medulla, the filaments in question being drawn darker, to show them up better. The drawing in itself is correct though misleading. It only represents a portion of the initial filament of the nemathecium, which in the other adjoining sections, had they been preserved, would have been seen to originate from cells just outside one of the antheridial cavities. Not unfrequently the spores seem later on to be drawn down into the antheridial cavities, and thus no trace of their external origin is left.

After entering the host by the ostiole of the antheridial cavity, the parasite immediately branches (Plate XVII., Fig. 1), the branches at first forcing their way into the internal medullary portion of the thallus of the host. Very soon a differentiation takes place in the primitive thallus

thus developed. In between the cells of the medulla the filaments of the parasite branch and some of them grow out in the direction of the cortex. These form the shoot-part of the plant, the former acting as root-portions. The filaments do not enter any cells of the host, but simply force their way in between them along the middle lamella. In some way, however, they become connected with the cells of the medulla of the host-plant, secondary pits being formed between the cells of both organisms.

The normal cells of the medulla of *Phyllophora* as a rule contain large quantities of starch. This store of food-material is the chief source of food for the parasite. The parasite, therefore, first of all, takes possession of this starch, and in older plants we find that the starch of the host has disappeared from the cells of the medulla, the cells of the parasite now being filled with starch. For this reason it is easy to differentiate the two organisms by adding iodine, when the parasite will turn dark blue, the cell-contents of the host remaining unstained.

From the filaments which are found in the medulla of the host arise, as already mentioned, the shoot-filaments. They grow in a direction chiefly towards the flat surface of the spermophores, which are infested by the parasite. The filaments soon reach the cells of the cortex, and passing out between the filaments of this layer, they branch outside the host, and gradually the nemathecium of *Actinococcus subcutaneus* (Lyngb.) K. Rosenv. is formed on the external surface of the host-plant. Numerous filaments arise from the root-portion, and by repeated branching the internal vegetative portion (intramatrical filaments) and the external portion (extramatrical filaments) assume large dimensions (Plate XVII., Fig 2). The external filaments form a mass of radiating rows of cells, often branched at the base, which in the end give rise to the tetraspores (Fig. 6).

The parasite is unable to pierce the outer covering of the host, when entering the latter. It can only attack the latter through the antheridial ostioles. On the other hand this outer coat is easily pierced when the same filaments are passing out to form the nemathecia. In this case they have a firm backing in the solid structure of the medulla of the host-plant. The apex of a filament which is passing through the outer wall of the latter seems to affect the surrounding substance in a peculiar way. This is otherwise quite homogeneous in structure, but

in places where it is being pierced, it seems to become vacuolated. It appears to be corroded in some way by the attacking filament of the parasite (Plate XVII., Fig. 3).

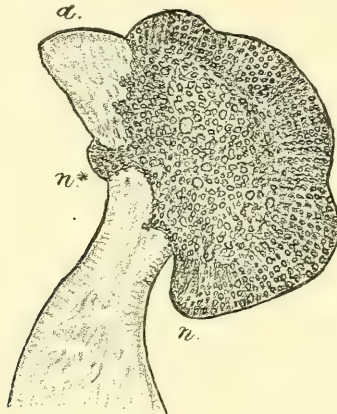


Fig. 6. *Actinococcus roseus* (Lyngb.) Kold. Rosenv. The shaded portion represents the parasitic nemathecium; the lighter portion is the thallus of the host-plant. *n.* large primary nemathecium; *n**. smaller secondary nemathecium just forming. $\times 40$ diam.

A large number of filaments pass out of the tissue of the spermophore within a certain limited space (Plate XVII., Fig. 4) On the outside of the spermophore they form dark-reddish bodies, the nemathecia of *Actinococcus subcutaneus* (Fig. 6). They are all joined together in a common gelatinous substance, in which they branch; the branches finally radiating outwards in a direction from the centre of the whole parasitic tissue.

At first as a rule these nemathecial bodies are formed only on one side of the flattened spermophore. Often, however, we see filaments arising from the intramatrical tissue of the parasite, which pass out on the opposite side of the spermophore (Fig. 6). When a second nemathecium is formed, it may be separate, if it is produced exactly opposite to the first; if it is produced close to the first nemathecium and next to it, the two frequently coalesce.

Ultimately, owing to the almost pseudo-parenchymatic development of the intramatrical tissue of the parasite, it is no longer possible in older specimens to distinguish between the filaments of the parasite and the ordinary tissue of the cortex and medulla of the host. As

already mentioned, the effect of adding iodine is to show up the cells of the parasite more clearly, as the latter has absorbed all the starch out of the cells with which it has come in contact. It is easy to make out the shape of the starch-grains of *Phyllophora* (2, p. 22, Fig. 26 n, 8—10), but impossible to detect any definite structure and shape in the case of the very minute elements composing the starchy mass found in the cells of *Actinococcus subcutaneus*. Those parts of the primitive thallus of the latter, which are presumably most actively growing, as, for example, the apices of the filaments of the shoot-portions, contain no starch or only very little indeed. The root-filaments are usually completely filled with starch.

The internal cells of the whole parasitic cushion vary much in size (2, Fig. 30). The smallest are barely $6\ \mu$ in diameter, the largest measure 60 by $30\ \mu$. The latter do not always belong to the parasite, but often form part of the tissue of the host. They are more or less round, the cells of the parasite being slightly elongated as a rule. The latter are connected with one another by fine cytoplasmic strands. The cells of *Phyllophora* also possess numerous pits, by means of which their cytoplasm is continuous. Only on rare occasions is it possible to make out any connexion between the cells of the parasite and the host. In cases where the parasite has been growing in the host for some time, the filaments of the former often may grow a considerable distance down into the tissue of the thallus of *Phyllophora* in order to absorb more food-material for the cells of the tetrasporic fructification.

The extramatrical filaments gradually form the nemathecium of the parasite. The outermost radially disposed filaments gradually develop into tetrasporangia. Each cell of these usually unbranched fertile threads, gives rise to four tetraspores, with the exception of the two to four apical cells (Fig. 7). The inner and lower cells of the fertile filaments also remain sterile. The whole fertile nemathecial layer is in itself about 150—200 μ deep. The sterile apical cells contain some clear, frothy cytoplasm and a distinct, though as a rule very much reduced, rhodoplastid. They are usually larger and longer than the tetrasporangia.

The tetraspores are formed by cruciate division, the first cross-wall formed being placed at right angles to the long axis of the fertile filament. The spore mother-cells measure $12 \times 16\ \mu$, the four nuclei being formed before the formation of cell-walls gives rise to the four tetraspores.

The tetraspores themselves are spherical in shape, and when escaping at maturity they measure 10—12 μ in diameter. They are

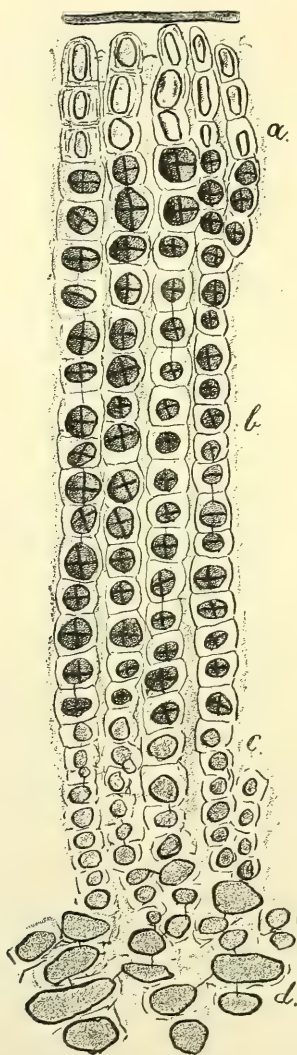


Fig. 7. *Actinococcus roseus* (Lyngb.) Kold. Rosenv. Vertical section of outer layers of nemathecium: *a*, sterile outer cells of nemathecial filaments; *b*, tetrasporangia; *c*, sterile inner cells, and *d*, the cells of the parasitic cushion. $\times 300$ diam.

surrounded by a very thin membrane, their cell-contents consisting of a very finely divided rhodoplastid and numerous starch-grains.

On arriving at maturity the nemathecium break up, the tetraspores are set free and presumably germinate. It is impossible as yet to say what actually is the fate of these tetraspores of *Actinococcus subcutaneus*, after they have been set free from the parasitic nemathecium. Do they germinate on another host and there form sexual plants with antheridia and procarpia?

The tetraspores ripen in December and January and shortly after are discharged from the nemathecium, some of the latter apparently continuing to vegetate for some time. With the appearance of the spermophores in the following autumn, we again find the parasite entering the host-plant. What have the spores been doing in the meantime? From what has already been said, it is not unlikely that what we see germinating on *Phyll. Brodiaei* in the autumn is really a carpospore.

It has been possible to follow out the germination of the tetraspores of our species of *Actinococcus*. Briefly the results obtained were the following (2, pp. 25—27, Fig. 32, 33). The tetraspores, derived from the nemathecium of *Actinococcus subcutaneus*, were sown on sterilized and purified parchment-paper. The whole was put in a small glass vessel filled with filtered seawater. Several cultures were started. The spores germinated, and in parts remained in a living condition for nearly two years. The products of germination took the form of small protonema-like organisms. The largest of these consisted of uniseriate filaments and larger aggregations of cells, which at the time I took to be the rudimentary basal attachment-disks of *Phyll. Brodiaei*: it consisted altogether of upwards of 250 cells. As yet it still remains to be seen what actually becomes of these products of germination. Possibly they would normally have attacked a new host, be this *Phyll. Brodiaei* or some perfectly different plant, on which ultimately the carpospores would possibly be formed. The carpospores perhaps, one might almost say probably, germinate on *Phyll. Brodiaei*, and eventually give rise to the nemathecium of *Actinococcus subcutaneus*. It is not to be wondered at that the parasite should be able to live separately for nearly two years in an artificial culture, when it is borne in mind that its cells contain rhodoplastids. The long filaments are probably searching for a suitable substratum, whereas the larger

aggregations of cells represent portions of the thallus which are chiefly assimilating. On the other hand, the form of the plants resulting from the experimental germination of the tetraspores of *Actinococcus* may be due to the very abnormal conditions under which germination took place.

In discussing the question a short time ago with Professor Reinke, the latter suggested as a possibility, which ought not to be dismissed *prima facie*, that *Actinococcus* might really be an asexual generation of *Phyll. Brodiaei*, growing parasitically on the sexual generation. Although this is not absolutely impossible, it is not very probable that it represents the true state of affairs. I need only recall to mind the fact that the contents of one antheridial cavity at least are destroyed by the parasite entering the host.

The foregoing paper was written for the purpose of definitely settling the nature of the pseudo-nemathecia of *Phyll. Brodiaei* (Turn.) J. Ag., of the *parasiticum quid* of Lyngbye, of *Actinococcus subcutaneus* (Lyngb.) K. Rosenv. and *Act. roseus* Ktz., all of which represent the nemathecia of *Actinococcus subcutaneus* (Lyngb.) K. Rosenv.

Other species of *Phyllophora* Grev. and of other closely related Gigartinaceae and other species of *Actinococcus* Ktz. and allied genera, are about to be examined by the author. It is a remarkable fact that the nemathecia of *Phyll. Brodiaei* have not yet been found, although this species is as common as *Phyll. membranifolia* (G. and W.) J. Ag., the nemathecia of which are frequently met with, even in the Baltic. It is necessary that this point also should be elucidated.

There are frequently found growing on specimens of *Phyll. Brodiaei* in the Baltic, and more rarely in other seas, certain structures, which have been called 'Traubenkörper' (1, p. 9). Tetraspores, antheridia and procarpia are found on these, but they never apparently attain to maturity. Schmitz also mentions these peculiar bodies, referring them provisionally as a new species to the genus *Actinococcus* Ktz. (5, p. 380). Kolderup Rosenvinge has described a new species of *Ceratocolax*, which apparently embraces the two organisms just mentioned, and to which he has given the name of *Ceratocolax Hartzii* K. Rosenv. (4, p. 34).

The following is a brief description of the genus *Actinococcus* Ktz. and species *Actinococcus subcutaneus*. It is my intention to give a complete list of synonyms, literature and exsiccata in a later paper; as also a discussion of the systematic position of this plant.

ACTINOCOCCUS Ktz.

Literature : (1) Darbish., Beitrage, p. 7, &c. ; (2) Darbish., Phyllophora-Arten, p. 36 ; (3) Gomont, p. 2, &c. ; (4) Kolderup Rosenvinge, p. 33 ; (5) Schmitz, Actinococcus, p. 392.

Thallus parasitic on other Florideae, the vegetative portion consisting of filaments branching in the interior of the host-plant (intramatrix portion), and fertile filaments forming a cushion of parasitic tissue on the external surface of the host (extramatrix portion of the thallus). Antheridia and procarpia unknown. Tetraspores formed by cruciate division in radially disposed rows of tetrasporangia.

ACTINOCOCCUS SUBCUTANEUS (Lyngb.) K. Rosenv.

Literature : (1—4) The same as of the genus ; (5) Schmitz, pp. 369-379.

Synonymy : Actinococcus roseus Ktz.

Thallus (asexual plant at least) parasitic on the young spermatophores of *Phyll. Brodiaei* (Turn.) J. Ag., which it enters through the ostiole of the small antheridial cavities. The intramatrix portion consists of longish cells in uniserial filaments, which branch in the medullary tissue of the host, forcing their way along the middle lamellae of the cells. The extramatrix portion is formed by filaments arising from the intramatrix tissue which break through the cortex and give rise on the external surface of *Phyllophora*, to a parasitic cushion of radially disposed rows of cells, which eventually develop into tetrasporangia. The outer and innermost cells of these fertile filaments remain sterile. The tetraspores are formed by cruciate division. Antheridia and procarpia are unknown. It is also not yet known what becomes of the tetraspores, and whether the spores which give rise to the parasitic nemathecium on *Phyll. Brodiaei* (Turn.) J. Ag. are tetraspores or carpospores.

In conclusion I have to express my thanks to the 'Kgl. Ministerial-Kommission z. Untersuchung d. deutsch. Meere in Kiel' for permission to make use of the *clichés* for the illustrations in the text of this paper.

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EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. Darbshire's paper on Actinococcus and Phyllophora.

Actinococcus subcutaneus (Lyngb.) K. Rosenv.

Fig. 1. Longitudinal section through the apical portion of a spermatophore of *Phyllophora Brodiaei*. The dark cells stained with iodine represent the cells of the parasite, which has entered the host through the ostiole of the antheridial cavity (at *a*). The parasite is branching in between the cells of the host. A differentiation is already visible in the former into a root and shoot portion. $\times 250$ diam.

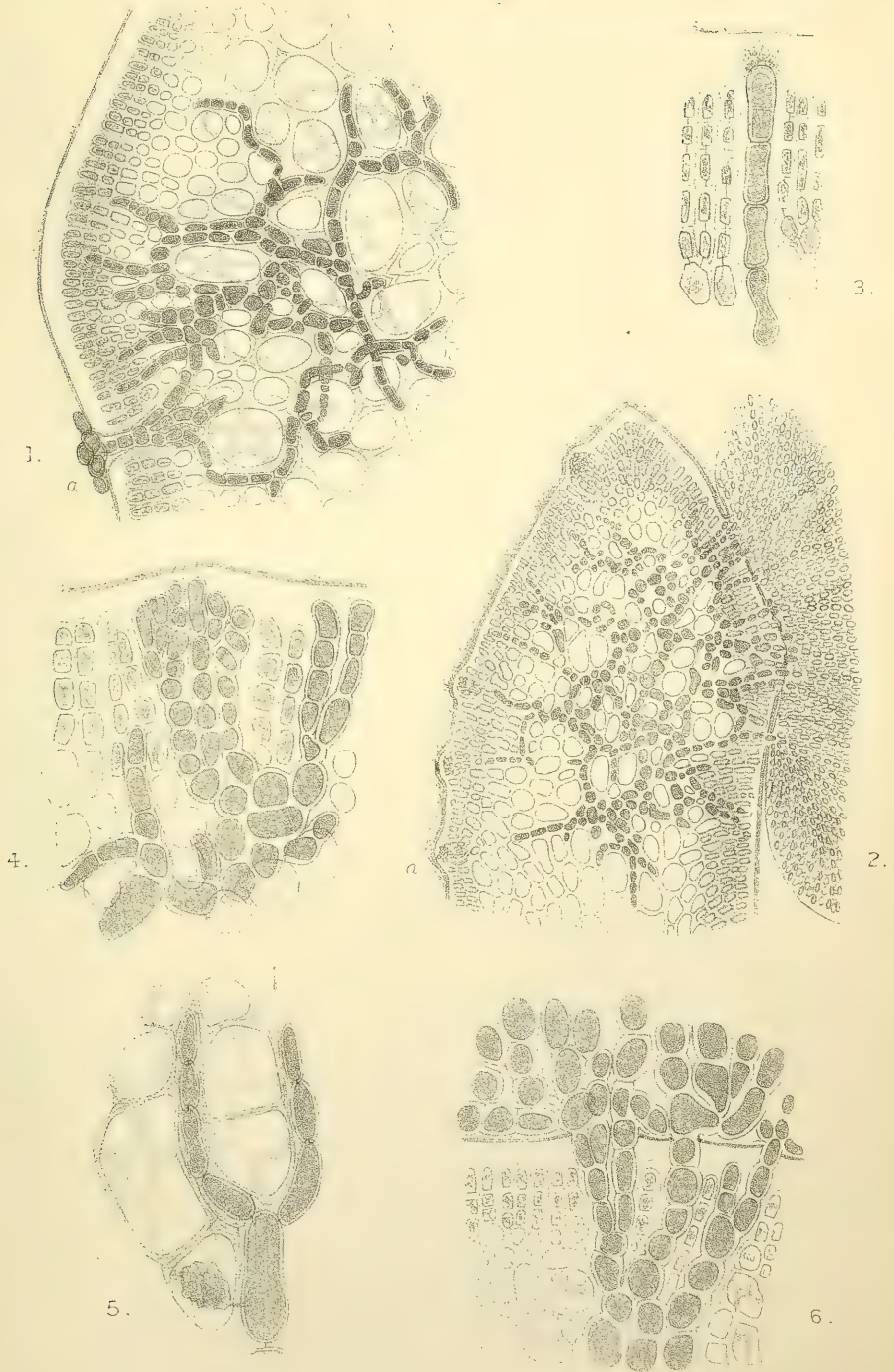
Fig. 2. General view of a longitudinal section through the apex of a spermatophore of *Phyllophora Brodiaei*, which has been successfully attacked by the parasite, *Actinococcus subcutaneus*. The intramatrical filaments, stained dark blue with iodine, are clearly seen. From these arise the extramatrical filaments, which have passed out of the tissue of the host, through the cortex. They have formed a nemathecium, only part of which is seen in the drawing. To the left of the section, at *a*, are seen four small antheridia-lined cavities. $\times 170$ diam.

Fig. 3. A single shoot-filament of the parasite breaking through the cortex of the host. The outer covering of the latter is apparently undergoing some change. $\times 400$ diam.

Fig. 4. A bunch of shoot-filaments of the parasite forcing their way through the cortex of the host. They are much branched. $\times 400$ diam.

Fig. 5. A branching filament of the parasite forcing its way between the medullary cells of the host-plant. The arrow points in the direction of the cortex. $\times 400$ diam.

Fig. 6. Section through the basal attachment of an older nemathecium, showing clearly the boundary between the host and the parasite. $\times 400$ diam.





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THE STRUCTURE OF *XENIA HICKSONI*, NOV. SP., WITH
SOME OBSERVATIONS ON *HETEROXENIA ELIZABETHÆ*,
KÖLLIKER.

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With Plates XVIII.—XXII.

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INTRODUCTION.

At the suggestion of Professor Hickson I undertook to examine a specimen of the the Alcyonaceous coral *Xenia*, which he had collected on the reefs of Talisse Island, North Celebes, chiefly with the intention

of working out the arrangement of the canals of the colony. As the investigation proceeded the preservation of the colony was found to be so exceptionally perfect that it seemed desirable to make a study of its histology, and as several new and interesting points were early observed I finally decided to work out in detail the complete anatomy and histology of the colony. Although many authors have described the external characters of various species of *Xenia*, few have paid any attention to their internal structure. Bourne (1895) has referred to the canal system, the mesogloea, and the distribution of spicules in two species of *Xenia*, and in *Heteroxenia Elizabetha*, and Kölliker (1874) described the anatomy of his new *Heteroxenia Elizabethæ* as far as its very imperfect preservation would permit. These two accounts contain practically the whole of our knowledge of the internal structure of these two genera, and hence, when the beautiful preservation of this colony of *Xenia* from Talisse was apparent, there was a strong inducement to attempt a more complete account of its detailed anatomy and histology.

The work has been carried on during the past two years in the zoological laboratories of the Owens College. My best thanks are due to Professor Hickson for the beautifully preserved specimen upon which most of my work has been done, and for advice and criticism given during the progress of the work. I am also indebted to Professor Lankester for a specimen of *Heteroxenia Elizabethæ*, to Mr. J. S. Gardiner for a specimen of *Xenia* from Rotuma, and to Dr. Arthur Willey for fourteen specimens of *Xenia* from various reefs in the Pacific.

EXTERNAL CHARACTERS OF THE COLONY (Pl. XVIII.).

The *Xeniidae* are distinguished from all other *Alcyonaria* by their soft, fleshy consistency and non-retractile polyps. The former character is due to the fact that their spicules are very minute rounded or oval discs, which have an organic basis impregnated with only a small quantity of calcium carbonate.

This colony arises from a single stem, which is slightly expanded at its point of attachment to the rock, and measures about 15 mm. in diameter at that point. This basal portion is very short and thick, and supports four main stems, all of which divide into two or more, producing altogether thirteen stems or branches ranging in length from about

10 mm. to 30 mm., and in breadth from about 4 mm. to 10 mm. The total height of the colony from the point of attachment to the tips of the highest polyps is 50 mm.

The polyps are, for the greater part of their length, bound together in bundles of about forty to sixty, each bundle forming one stem of the colony. The free portions of the polyps arise from the slightly expanded umbrella-shaped area at the distal end of each stem. Many of the polyps stand almost perpendicularly to the convex disc, but those near the edge of the disc hang downwards towards the base of the colony. The polyps are closer together near the edge of the umbrella, being here .5 mm. to .7 mm. apart, whereas in the middle of the umbrella they are 1 mm. to 2 mm. apart.

Polyps (Pl. XIX., Fig. 2).—The polyps, or, more correctly, the free portions of the polyps, are non-retractile and moderately long and slender. The tentacles are half to two-thirds as long as the body of the polyp. Each tentacle bears on its inner side numerous short, conical elevations with rounded ends. These correspond to the pinnules found on the tentacles of other *Alcyonaria*.

The colour of the colony in spirit is light brown.

As mentioned above, the free portions of about forty to sixty fully developed polyps project from the umbrella-shaped area at the distal end of each stem, but besides these there are several younger polyps or buds in various stages of development, and these are invariably situated on the edge of the umbrella.

In fully developed specimens the following are the measurements :—“Body” of the free portion of the polyp 4 mm. to 7 mm. long, and 1.0 mm. to 1.2 mm. broad. Tentacles 2 mm. to 5.7 mm. long, and .75 mm. broad. The total length of the adult polyps is thus 6 mm. to 12 mm.

The body of the polyp is cylindrical and its wall moderately strong. In several of the *Xeniidae* the body-wall of the polyp is so weak that when the colony is taken out of spirit the polyps fall together into a mass. In this species, however, the body-wall is just strong enough to support the polyps in an upright position, so that on removing the colony from spirit the polyps do not hang limply, but remain standing approximately in their natural positions.

Tentacles and Pinnules (Pl. XIX., Figs. 2 and 3).—Each polyp bears eight tentacles, each of which is provided with numerous pinnules.

The pinnules on each side of the middle line of the tentacle are arranged in three longitudinal rows, and they form also somewhat oblique transverse rows of three pinnules rising from the oral towards the aboral side of the tentacle (Fig. 3, *D*). When the tentacle is viewed from the inner or oral aspect, all the pinnules are generally visible (Fig. 3, *B*, *D*), but on the outer or aboral side of the tentacle only the outer longitudinal row of each side is, as a rule, seen (Fig. 3, *A*, *C*). The pinnules are often clearly separated into the two series of three rows in each by a narrow area which extends along the middle line of the inner face of the tentacle, from the base to within a short distance of the tip (Fig. 3, *D*). This area, free from pinnules, may be .25 mm. across, and may often be traced to within 1 mm. of the tip of the tentacle. In other specimens, however, it is entirely obliterated, and the median pinnules of the two series are in contact with each other, at any rate at their bases. The width of this area varies, not only in separate individuals, but in the different tentacles of the same individual. These variations are probably due to the different degrees of contraction of the tentacles on killing, and the condition in which the free area is well marked is seen only in those tentacles which have been killed in an expanded condition.

At the tip of the tentacle the pinnules are smaller than those in the middle. They are arranged more or less in two series, one on each side of the middle line of the tentacle, but three rows on each side are not distinguishable; at a distance of about 1 mm. from the tip of the tentacle, however, the typical arrangement of two series, with three rows of pinnules in each, is gradually assumed (Fig. 3, *B*).

At the base of the tentacle the pinnules are much smaller but have the typical arrangement, except in the case of one or two of the proximal transverse rows. Here the pinnules appear to be in course of formation, the outer ones being formed first, the inner ones developing from without inwards (see Fig. 3, *D*).

On looking at the tentacle from the outer side only the outermost row of pinnules is usually visible. These, which are about twelve to twenty in number on each side, are set close together and point towards the tip of the tentacle (Fig. 3, *A*). At the tip of the tentacle the arrangement of the pinnules may be well studied, and, as in *Aleyonium* (Hickson, 1895), they are not paired (Pl. XIX. Fig. 2). The pinnules are conical elevations with rounded ends. Those in the

middle portion of the tentacle are about .5 mm. long and .15 mm. to .2 mm. broad, but those nearer the base and tip are smaller. The pinnules when fully expanded are about three times as long as they are broad, and each tapers gradually from its base to its blunt, rounded tip. When slightly contracted the pinnule is somewhat swollen at its base, and if further contracted becomes more swollen and globular at its base as its length decreases. Although the body of the polyp is non-retractile, the tentacles are often found slightly contracted, being in many cases curled inwards over the mouth. Several examples of tentacles in this condition are shown in Fig. 1.

DIAGNOSIS OF THE SPECIES *XENIA HICKSONI*.

The species of *Xenia* are distinguished from each other by the general form of the colony, the size of the polyps and tentacles, the number of rows and shape of the pinnules, and the presence or absence of an area free from pinnules, on the inner face of the tentacle.

After careful comparison with the accounts of all the hitherto described species, I am unable to refer this specimen to any of them, and therefore I have established for it a new species with the name *Xenia Hicksoni*. Its characters are as follow :

The colony consists of several cylindrical, usually branched stems, arising from a single thick stem or base. The stems range in length from 10 mm. to 30 mm., and in breadth from 4 mm. to 10 mm. From the arched or convex summit of each stem the free parts of the polyps arise. These are smaller and moderately close together near the edge of the summit, but larger and further apart in the middle of the arched end. The polyps (including tentacles) measure 6 mm. to 12 mm. in length, and 1 mm. to 1.2 mm. in breadth. The tentacles are moderately slender and 2 mm. to 5.7 mm. long. Each tentacle bears on the inner side two series of pinnules, each series consisting of three rows of twelve to twenty pinnules in each row. There is usually a narrow area free from pinnules extending along the middle line of the tentacle to within about 1 mm. of the tip. The pinnules are conical elevations with rounded ends. Those in the middle of the tentacle are about .5 mm. long, and are about three times as long as they are broad ; those nearer the base and tip of the tentacle are somewhat shorter. The body-wall of the polyps is moderately thick, and is strong enough to

support the polyps in their natural position when the colony is removed from the spirit. The spicules are round or oval discs measuring .012 mm. to .022 mm. in length, .006 mm. to .013 mm. in width, and about .004 mm. in thickness. They are numerous in the ectoderm of the stem and of the body of the polyp, but are practically absent from the tentacles and pinnules.

Round the edge of the umbellate summit of each stem are a few buds or young polyps in early stages of development. The specimen is light brown in colour (in spirit).

Habitat.—The reefs of Talisse Island, North Celebes.

This species appear to differ from most, if not all other species of *Xenia* in the absence of spicules from the tentacles and pinnules. In general form of the colony this specimen most resembles *X. umbellata*, Savigny, but it differs from the latter in possessing smaller polyps, with much shorter and stouter pinnules, which do not leave the axis of the tentacle free along its whole length (cf. Klunzinger, 1877, Pl. 3, Fig. 3a).

GENERAL ANATOMY.

Stomodæum and Mesenterial Filaments.—In the centre of the oral disc of each polyp there is a funnel-shaped depression about one-third of a millimetre in depth leading to the mouth. This depression is formed by partial contraction of the oral disc; if the polyp were fully expanded this depression would not exist, but the mouth opening would be level with the oral disc. The mouth (*Mo.*) leads into the stomodæum (*St.*), which is 1.8 mm. to 2.2 mm. long. The stomodæum is long compared with the length of the free portion of the polyp, and in longitudinal section presents a striking appearance, running down, as it does, so far into the cœlenteron. The stomodæum is oval in transverse section, being somewhat flattened from side to side. It has a well-marked ventral groove or siphonoglyph (*Si.*), the cells of the lower third of which bear long flagella (*F.*). The groove is not as well marked in the upper as in the lower portion of the stomodæum, and is scarcely discernible at the mouth opening. The columnar epithelial cells forming the siphonoglyph are, as is usual, longer than those of the rest of the stomodæum, and these cells bear very long flagella (.07 mm.), which in some examples extend almost to the centre of the cavity of the stomodæum. The epithelium of the rest of the stomo-

dæum is smooth and not folded in any way. Many of these epithelial cells bear short cilia on the free surface, but among these are numerous

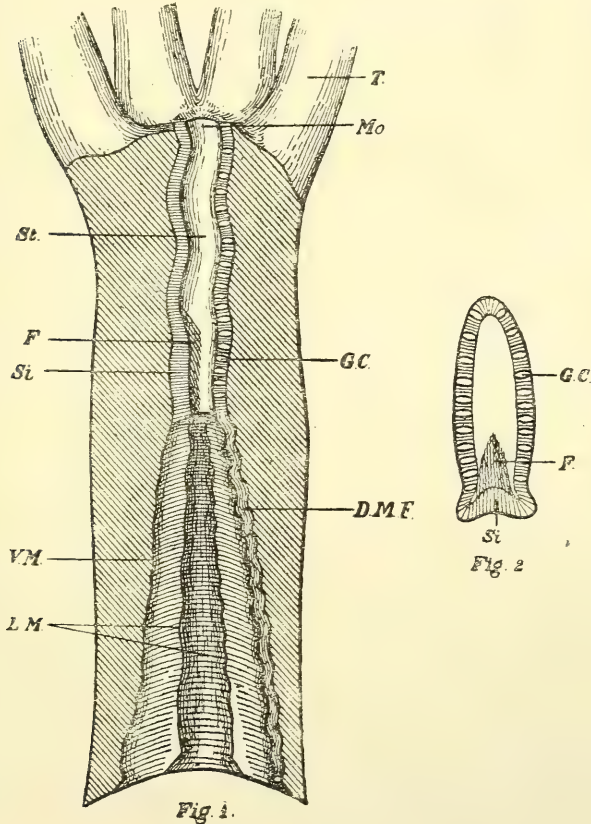


FIG. 1.—Semi-diagrammatic view of one half of a polyp which has been cut along the dorso-ventral line. Only the bases of the tentacles are shown $\times 20$.

Fig. 2.—Transverse section through the lower third of the stomodæum (about the level of the reference letter *F* in Fig. 1) $\times 80$.

D.M.F. Dorsal mesenterial filament on the edge of the dorsal mesentery; *F*. Flagella of siphonoglyph; *G.C.* Gland cells of stomodæum; *L.M.* Edge of lateral mesentery (mesenterial filament absent); *Mo.* Mouth; *Si.* Siphonoglyph; *St.* Stomodæum; *T.* Tentacle; *V.M.* Edge of ventral mesentery (mesenterial filament absent).

cells (*G.*), which are, like goblet-cells, swollen or flask-shaped, due to the presence of some secretion to which they give rise. These cells generally appear to be empty, having discharged their secretion, which in some cases can be seen issuing from the cell into the cavity of the stomodæum (Pl. XXI., Fig. 18). These secreting cells occur chiefly in the middle and lower portions of the stomodæum, and are most abundant on the lateral walls near the siphonoglyph. They do not occur among the cells which form the siphonoglyph (Pl. XX., Fig. 10). Secreting cells have not hitherto been noticed in the stomodæum of the *Alcyonaria* (Ashworth, 1898).

These goblet-cells of the stomodæum are the only secreting cells connected with the digestive cavity, as the six thick short ventral and lateral mesenterial filaments, which bear the gland-cells in other *Alcyonaria*, are absent in all polyps of this *Xenia* (see Woodcut, p. 187). Only the dorsal mesenteries possess thickened edges, forming two mesenterial filaments (*D.M.F.*) which have a similar course and structure to those of *Alcyonium*. The free edge of the ventral and lateral mesenteries is only very slightly thickened, and the thickening is due entirely to the greater amount of mesogloea present at the edge of the mesentery. The cells which cover the edge differ in no way from those which cover the remaining portions of the mesentery.

New points in the anatomy of this *Xenia* are the presence of gland-cells in the stomodæum, and the absence of the six ventral and lateral mesenterial filaments usually present in the polyps of the *Alcyonaria*. Wilson (in *Kophobelemnion*, 1884) and Hickson (in *Alcyonium*, 1895) have shown that these mesenterial filaments bear the cells which produce the digestive secretion. I would suggest that the absence of these filaments in this *Xenia* is correlated with the presence of gland-cells in the stomodæum, and that the latter, judging from their appearance and position, perform some digestive function. As mentioned above, the cells are most abundant on the ventro-lateral walls of the stomodæum, near the siphonoglyph. As the flagella of the siphonoglyph create an inward current of sea water carrying food particles, which passes along the ventral groove, the greater abundance of secreting cells in the walls abutting on this groove is suggestive of the digestive function of the secretion, which can readily be poured out on to the ingoing food particles.

The siphonozooids which occur in some other *Alcyonacea* (e.g., *Sarcophyton*) and in Pennatulids are the only recorded examples of polyps in which the ventral and lateral mesenterial filaments are absent. According to Wilson (1884), these siphonozooids derive their food supply from the autozooids or feeding polyps, the dorsal mesenterial filaments of the former creating upward currents which cause a flow of fluid from the autozooids to the siphonozooids, through the canals which connect them together. Food undergoes digestion in the autozooids, and some of the products are passed on to the siphonozooids, hence the latter do not require cells to produce a digestive secretion.

In this *Xenia* the secretion in connection with the digestive cavity is formed, not by endoderm cells, but by cells which are derived from the ectoderm, as from a study of the buds I have found that the stomodæum is ectodermic in origin in this as it is in other *Alcyonaria* (Wilson, 1883). Since the absence of ventral mesenterial filaments in *Xenia Hicksoni* was proved I have carefully examined all the other specimens of *Xenia* at my disposal. These are sixteen in number, viz., one from Talisse Island, North Celebes, one from Rotuma, Fiji Islands, and fourteen from various reefs in the Pacific. In all these the ventral and lateral mesenterial filaments are absent, there being only a very slight thickening of the free edges of the mesenteries, this thickening being entirely due to a slight increase in the amount of the mesogloea along the free edges. In all the specimens the two dorsal mesenterial filaments are present and have the typical course and structure. In *Heteroxenia Elizabethæ* the two dorsal mesenterial filaments only are present. The absence of ventral and lateral mesenterial filaments may, therefore, be considered as one of the characters which distinguish the polyps of the genera *Xenia* and *Heteroxenia* from those of other *Alcyonaria*. In two at least of the specimens of *Xenia*¹ from Dr. Willey's collection some of the cells of the stomodæum are goblet-like, and similar to those described above in the stomodæum of *Xenia Hicksoni*.

Cœlentera of Polyps.—The other parts of the colony present a structure similar, in the main features, to that of other *Alcyonaria*. The polyps are, for the greater part of their length, bound together in bundles of about forty to sixty, each bundle

¹ *X. crassa*, Schenk, and *X. viridis*, Schenk.

forming one stem of the colony. The external characters of the free portion of the polyp have been described above. The eight mesenteries of the polyp are arranged as in typical *Aleyonaria*. On their ventral faces they bear the retractor muscles, and on the opposite faces the protractor muscles, neither of which are well developed. This somewhat feeble development of retractor and protractor muscles accounts for the non-retractile nature of the polyps. The intermesenterial spaces are continued upwards into each tentacle and into each pinnule. In the free portion of the polyp, and particularly in the tentacles and pinnules, these spaces are to a large extent filled up by zooxanthellæ. The specimen is a male, and in the lower part of the free portion of the polyp, and in the upper part of the stem, the cœlentera are crowded with sperm-sacs containing spermatozoa in all stages of development, from the small masses containing only two or four primitive sperm-cells to the large mature sperm-sacs containing many hundreds of ripe spermatozoa.

Mesogloea, its Canals and Cells.—In the stems the cœlentera of the polyps are bound together by a moderately large quantity of mesogloea. The mesogloea immediately round each polyp is slightly denser than that further away, so that in transverse sections of the stem, especially if the sections be taken through the upper part, one can distinguish the more deeply staining ring of slightly denser mesogloea, which definitely belongs to the cœlenteron within it, from the less dense mass of mesogloea between these rings, which cannot be assigned to any polyp or polyps (Plate XX., Fig. 9). Traversing the mesogloea of the stem are numerous canals, cords and strands of cells, which place all the parts in intimate communication with each other. The canals may be divided into two systems—a superficial system and an internal system.

The superficial canal system (Figs. 8, 9, *Sup. Can.*) is formed by a plexus of numerous endodermic canals, which are situated in the outer portion of the mesogloea, just beneath the ectoderm of the stem. This system of canals extends all round the cylindrical stems, and also runs on the umbrella-shaped areas from which the free portions of the polyps arise (Fig. 8). The cavity of this system of canals is invaded throughout by zooxanthellæ, which are especially numerous in the canals in the upper part of the stem.

The internal canal system consists of a series of longitudinal canals (Figs. 8, 9, *Long. Can.*) which run generally in a sinuous or zigzag course in the mesogloea, between the coelentera of the polyps. These canals lie in the mesogloea, almost equidistant from the surrounding coelentera, and they run in this position from the top of each stem to the base of the colony. These canals are also endodermic, and have usually only a small lumen. They communicate with the coelentera of the polyps, with the superficial canal system, and with each other.

At the base of the colony the canal system is exceedingly complicated, due to the numerous branchings and anastomoses of the canals. The coelentera are continued down to the base of attachment of the colony, where they are in communication with the numerous branches of the canal systems. The coelentera are readily distinguishable from the canals by their greater size, and the presence in them of eight small ridges, to which the mesenteries in this region are reduced. Besides the superficial and longitudinal canals briefly described above, there are in connection with the longitudinal canals numerous small lateral or transverse canals, with small lumen, which pass from the canals either to other neighbouring canals or to the coelentera (Figs. 8, 9). The coelentera of the polyps do not open into each other directly, but are indirectly connected by these canals.

The base of the cylindrical main stem is somewhat flattened out, and this basal portion is hard and horny; and, being closely applied to the rock, provided a firm basis upon which the other parts of the colony were supported.

ECTODERM.

The ectoderm is a moderately thick layer, in which large columnar and smaller interstitial cells may with difficulty be distinguished. If a section of a tentacle or pinnule, which was well expanded at the moment of killing, be examined, the ectoderm is then seen to consist of a row of cells elongated at right angles to the free surface, below which are smaller rounded cells which probably correspond to the interstitial cells of the ectoderm of *Alcyonium* and other coelentera. (Pl. XX., Fig. 11).

The protoplasm of the ectoderm cells is very finely granular; occasionally cells are met with containing a few small vacuoles.

Many of the ectoderm cells of the tentacles and pinnules are produced at their inner ends into muscle processes which lie in the outer portion of the mesogloea, parallel to the free surface. These muscles are all longitudinal in direction. The ectodermic muscles of the tentacles are much more strongly developed on the oral than on the aboral side, especially at the base of the tentacles, where the muscles of the oral side form a strong band beneath the cells quite eight times as thick as the band of the muscles on the aboral side. Nearer the tip of the tentacle the muscles of the two sides become almost equal.

In the body of the polyp ectodermic muscles are present only in the distal portion around the base of attachment of the tentacles and for a distance of about a millimetre below this point. Myo-epithelial cells are absent from the ectoderm of the stem. The absence of muscle-cells from the ectoderm of the stem and the greater portion of the body of the polyp is connected with the non-retractile character of these parts. Their presence in the tentacles, pinnules and distal portion of the body of the polyp confers on these parts some power of contraction, and an examination shows that the pinnules and tentacles vary somewhat in length and shape, and that the tentacles are often turned inwards over the mouth, due to the contraction of the muscles of the oral side. The absence of spicules from the tentacles and distal portion of the polyp renders the ectoderm softer and more pliable, and therefore more readily acted upon by the contraction and expansion of the muscle processes of its cells.

Among the ordinary columnar cells there are in the ectoderm of the stem and the body of the polyp large swollen cells which probably secrete the mucus which thinly covers the external surface of most of these parts (Pl. XXI., Fig. 17, *Muc. C.*). These mucus-cells are large and abundant in the angle of the Y-shaped piece formed where a stem divides.

The ectoderm cells present on their outer side a moderately plane surface, but on the inner side a more irregular one, as numerous processes pass from the cells inwards and establish communication either with the endoderm or with cells lying deeper in the mesogloea (Fig. 17).

On reaching the base of the colony the ectoderm curves inward, and was applied to the face of the rock to which the colony was attached.

The stomodæum is ectodermic in origin in this as in other *Alcyonaria* (Wilson, 1883), as may be seen from a study of the buds. The presence of a ventral ciliated groove and of gland-cells and other features of its structure have already been referred to (p. 251). The ectoderm of the stomodæum and the adjacent endoderm are connected by numerous cells or strands of cells passing through the thin mesogloal lamina which separates the two cell layers (Pl. XXI., Fig. 18).

The ectoderm cells give rise to nematocysts and spicules.

Nematocysts.—The nematocysts are exceedingly numerous in the ectoderm of the tentacles and pinnules (Pl. XX., Fig. 11, *Nem.*); there are large numbers in the ectoderm of the body of the polyp, rather fewer in the ectoderm of the stem, and a few in the ectoderm of the oral disc, in the funnel leading to the mouth, and also in the upper part of the stomodæum. The nematocysts are, as in other *Alcyonaria*, exceedingly small, their length being $\cdot 008$ mm. and their breadth $\cdot 002$ mm. to $\cdot 003$ mm. They have bluntly pointed ends and are circular in transverse section. Each nematocyst is formed in a cnidoblast cell (Pl. XX., Fig. 12, *Cn.C.*), the nucleus and protoplasm of which lie flattened against the capsule on one side and a little nearer the inner than the outer end of the capsule. The filament or thread lies coiled up inside this capsule, there being about twelve coils distinguishable in the most favourable specimens. The thread appears to be quite simple, there being no barbs visible. Its length when shot out would probably be about $80\ \mu$ ($\cdot 08$ mm.). The nematocysts are usually placed with their long axes at right angles to, and their bluntly pointed ends level with or slightly projecting from, the free surface of the ectoderm. This can be especially well seen in sections of the tentacles and pinnules (see Fig. 11). The nematocysts stain deeply with thionin, hæmatoxylin, and especially with iron hæmatoxylin (Heidenhain). Iron hæmatoxylin is exceedingly useful for staining the small nematocysts of *Alcyonaria*; in fact, without some good staining reagent it would be very difficult to find the minute capsules in many cases. Moseley (1881, p. 119) wrote that "no nematocysts were found in *Sarcophyton*," but by using the iron hæmatoxylin stain I have found them in sections passing through the ectoderm of the tentacles. They are very similar in shape to those of *Xenia Hicksoni*, but smaller in

size, being only $6\ \mu$ to $7\ \mu$ long and $2\ \mu$ wide. The nematocysts of *Alcyonaria* are all very small, as may be seen from the following table :

<i>Sarcophyton pauciflorum</i> ¹	$6\ \mu$ — $7\ \mu$ long and $2\ \mu$	wide (J. H. A.)
<i>Alcyonium digitatum</i> - -	$7\frac{1}{2}\ \mu$ „ „	$2\ \mu$ — $3\ \mu$ „ (Hickson)
<i>Xenia Hicksoni</i> - - -	$8\ \mu$ „ „	$2\ \mu$ — $3\ \mu$ „ (J. H. A.)
<i>Heteroxenia Elizabethae</i> -	$9\ \mu$ „ „	$2\frac{1}{2}\ \mu$ „ (J. H. A.)
<i>Clavularia viridis</i> - - -	$9\ \mu$ — $10\ \mu$ „ „	$2\ \mu$ — $3\ \mu$ „ (J. H. A.)
<i>Heliopora cœrulea</i> - - -	$9\ \mu$ „	(Moseley)
<i>Clavularia prolifera</i> - -	$10\ \mu$ — $15\ \mu$ „	(v. Koch)

Spicules (Pl. XX., Figs. 13—15 ; Pl. XXI., Fig. 16).—The spicules, the form of which was compared by Kölliker to that of red blood-corpuscles, are rounded or oval discs. which are, however, sometimes bilobed (Fig. 13). They are $\cdot 012$ mm. to $\cdot 022$ mm. long, $\cdot 006$ mm. to $\cdot 013$ mm. broad, and $\cdot 003$ mm. to $\cdot 005$ mm. thick.

Spicules are absent from the tentacles and pinnules of all the polyps examined except one. In the latter a few small spicules (about $8\ \mu$ to $12\ \mu$ long) are present in the ectoderm of the tentacles, but only in the proximal $\cdot 4$ mm.

In the deeper part of the ectoderm, just below the point of attachment of the tentacles, spicules are present in small numbers, while in the middle and proximal portions of the body of the polyp they are very numerous, a tangential section of the body-wall in this region showing that the spicules form an almost complete layer in the deeper part of the ectoderm. Spicules are numerous in the ectoderm of the stem, and especially numerous in the angle of the Y-shaped piece formed at the point of division of a stem. In the lowest parts of the colony, *i.e.*, in the portion attached to the rock, they are present in enormous numbers, practically filling the entire mesogloea in that region. The largest examples of spicules are to be found in the basal portion of the colony. (Those shown in Fig. 13 are from this region.) The absence of spicules from the tentacles, pinnules, and from the body of the polyp around the base of the tentacles is correlated with the power of contractility, slight though it is, which is possessed by these parts. The presence of an almost complete layer of spicules forming a more or less rigid cylinder in the middle and proximal portions of the body of the polyp and in the stem, together with the absence of muscle

¹ *S. pauciflorum*, Ehrenberg = *Lobophytum pauciflorum*, v. Marenzeller, 'Zool. Jahrb.,' i., 1886.

processes from the ectoderm cells of these portions, sufficiently accounts for the non-retractile character of these parts of the colony. The increased number of spicules in the angle between two branches gives the required rigidity to this part, and prevents flexure of the branches and consequent closure of some of their canals and coelentera.

Besides the extraordinary number of spicules present in the ectoderm and mesogloea of the last few millimetres of the base of the colony, this part is further strengthened by much of the mesogloea becoming converted into a dense and horny substance, so that the part of the colony attached to the rock is hard and quite different to the touch from any other part of the colony. This hard base would afford a firm attachment and a rigid support to the branches which arise from it.

The spicules are formed within cells which at first lie in the deeper parts of the ectoderm or have migrated into the outer parts of the mesogloea (Fig. 16). The arrangement of the spicules is not very regular, as they appear to present to the free surface their edge or their flat face indifferently. In nearly all preparations the nucleus and remains of the protoplasm of the spicule-forming cell can be seen. The spicules, which have a horny consistency, have an organic basis impregnated with only a very small amount of calcareous matter. They stain deeply with hæmatoxylin, especially with hæmalum. They do not dissolve when treated with acids, but shrink very slightly, probably owing to the solution and extraction of the small amount of calcareous matter which they contain. They do not offer any difficulties in section-cutting, as the razor cuts through them with little resistance, and sections $2\ \mu$ to $4\ \mu$ in thickness may be readily obtained, although the specimen has not been previously decalcified. On this account *Xenia* offers exceptional facilities for the study of the development of spicules. As mentioned above, each spicule is formed within a cell lying in the deeper part of the ectoderm. When the young spicule first makes its appearance in the cell its substance is scarcely distinguishable from the protoplasm of the cell; in fact, it is not until the spicule has attained a diameter of $3\ \mu$ to $4\ \mu$ that it is possible to clearly differentiate it (Pl. XX, Fig. 15). The young spicule is then a small disc which stains with hæmatoxylin like the protoplasm of the cell, but its homogeneous structure enables the observer to distinguish it from the finely granular cell-protoplasm which surrounds it. From

this stage the spicule grows regularly in length and thickness, and the protoplasm of the cell covering it becomes gradually thinner until, in a fully formed spicule, this protoplasmic sheath forms an exceedingly thin investment, in which at one part may be seen the small, somewhat flattened nucleus embedded in a small mass of protoplasm (Figs. 13 and 14). In all the specimens, many hundreds in number, which I have examined, the spicule develops in a single cell with one nucleus. I have not been able to find any examples which showed that two cells or two nuclei were concerned in the formation of the spicule (cf. v. Koch's account of the development of the spicules of *Clavularia prolifera*, 'Morph. Jahrb.,' vii, p. 473, 1882).

MESENTERIES (Pl. XXI).

Mesenterial Filaments.—The stomodæum leads into the cœlenteron of the polyp, which is subdivided by the usual eight mesenteries (Pl. XX, Fig. 10). Of these only the two dorsal ones possess thickened edges or mesenterial filaments (Pl. XXI., Fig. 19). The free edge of the remaining six mesenteries is only very slightly thickened, this being due entirely to the presence of a slightly greater amount of mesogloea near the free edge of the mesentery. The cells which cover this thickened portion differ in no way from those covering the other parts of the mesentery (Pl. XXI., Fig. 20). The six ventral and lateral mesenterial filaments usually present in the polyps of the *Acyonaria* are not found in this genus. The dorsal mesenterial filaments arise from the lower edge of the stomodæum and run in a sinuous course along the dorsal side of the cœlenteron. In the primary polyps they may be traced to the base of the colony. In transverse section the filament is slightly bilobed, *i.e.*, there is a groove (of slightly varying depth) extending all the way down the middle of the free surface of the filament (Fig. 19). The cells on each side of this groove bear long cilia (0.075 mm.). The dorsal mesenterial filaments are quite typical, and agree well with the accounts given of those of other *Acyonaria* by Wilson and Hickson. They are probably ectodermic in origin, as they appear to be formed as two downgrowths from the inner end of the stomodæum. The cells of the filaments agree in structure with those of the stomodæum, being finely granular and non-vacuolated, and differing markedly from the much vacuolated neighbouring endoderm cells.

Muscles.—The retractor muscles are situated on the ventral faces of the mesenteries and the protractor muscles on the dorsal faces, as in *Alcyonium*. These muscles are somewhat feebly developed, as might be expected from the non-retractile nature of the polyps. Shortening of the retractor muscles produces a slight contraction of the oral disc and consequent formation of the funnel-like depression leading to the mouth, to which reference has already been made (p 251).

Cells in Mesogloea of Mesenteries.—On examining a transverse section through the mesenteries, there is seen to be a considerable quantity of mesogloea between the two endodermic lamellæ covering the mesentery (Fig. 20). In this mesogloea there are cells which have the reticulate protoplasm and general appearance of endoderm cells. These cells migrate into the mesogloea from the endoderm covering the surface of the mesentery, and even in a young polyp .8 mm. long a few cells have already taken up their position in the mesogloea. In older polyps there is a larger number of these cells in the mesogloea of the mesentery, though they are not equally numerous in all parts. In the upper portion of the polyp, about the level of the stomodæum, the mesogloea cells are few in number and small in size, but from this part downwards their number and size gradually increase, until in the mesenteries in the upper portion of the stem they are large and numerous, and in some cases completely fill up the mesogloea, so that the mass of cells is in close contact on both sides with the endoderm covering the two sides of the mesentery. Towards the base of the stem the cells become fewer in number and slightly smaller in size. These cells are found in the mesogloea of all the mesenteries, but they are less numerous in the dorsal mesenteries than in the remaining six. Many of the cells are at first somewhat elongated or pear-shaped, with one or more processes in connection with, or pointed towards, the endoderm; but later many of them become rounded and larger, and their nuclei become much larger.

The primitive genital cells are derived from these large rounded cells in the mesogloea of the mesenteries at the base of the polyp and in the upper portions of the stem. That this is the case is shown by the following:

- (1) These cells are most numerous in those parts of the colony where gonads occur in greatest numbers.

(2) In many cases one of these cells, surrounded by a thin film of mesoglœa, may be seen enclosed in a follicle of endoderm projecting from the edge of the mesentery. These are exactly similar to the neighbouring follicles which contain spermatozoa in various later stages of development.

(3) The nuclei of most of these cells are large and spherical, more vesicular than the nuclei of the adjacent endoderm cells, and resemble the nuclei of the genital cells (see Pl. XXII., Fig. 30).

(4) The ripe spermatozoa are situated in a follicle covered by a thin mesoglœal lamina, as well as by the endoderm cells outside this, *i.e.*, the ripe spermatozoa are situated in the same layer as these cells, *viz.*, in the mesoglœa.

The migration of genital cells from the endoderm of the mesenteries into the mesoglœa is similar to that described by O. and R. Hertwig in *Actinice* ('Die Actinien,' Jena, 1879, p. 95, and Pl. 7).

ENDODERM (Pl. XXI.).

The endoderm cells lining the cœlentera and the cavities of the tentacles have a similar structure throughout the colony. They are cubical or columnar, and contain many small vacuoles which give the protoplasm a reticulate appearance.

Cells which bear Flagella (Figs. 20—25, 27).—Among the ordinary endoderm cells there are numerous cells, the inner or free end of which is produced into a long process, which is from four to eight times as long as the basal portion of the cell. This process may be slender or moderately stout, and its length may vary in different specimens from .015 mm. to .12 mm. The basal part of the cell from which the process arises has the reticulate protoplasm of an ordinary endoderm cell, and the nucleus of the cell is situated in this portion. The process is not vacuolated, and for the greater part of its length its protoplasm exhibits a homogeneous or very finely granular structure. Its basal part, *i.e.*, the part in continuity with the vacuolated portion of the cell, stains deeply with hæmatoxylin, and in most cases shows very faint longitudinal striations which are visible only in the proximal third of the process.

The processes usually taper towards their free end, but in one instance this end is slightly broadened and flattened (Fig. 25 A). In

one case the process, which is a very large one, bears a short branch near the middle of its length (Fig. 25, *B*). This is the only branched process found among many hundreds examined. The processes of most of the cells project outwards almost at right angles to the free surface of the endoderm (Figs. 20, 21, 23, 24), but there are many similar to the one drawn in Fig. 22, in which the process is strongly curved and apparently moderately flexible.

These curious processes are very numerous, and are found in all parts of the endoderm lining the coelenteron and tentacles, but are most abundant in the portion of the coelenteron situated in the body of the polyp and in the upper part of the stem (Pl. XX., Fig. 9).

The nature of these processes is difficult to determine. In the preliminary note to the Royal Society (1898, written in February) I called them pseudopodia, but further investigation shows that the word *flagella* would probably better express their nature. The processes appear to be permanent, to have a moderately definite shape gradually tapering from base to tip, and to be flexible. The word pseudopodia implies more temporary structures with many different and continually changing shapes, while the term flagella implies tapering whiplash-like processes of more permanent and definite shape. The homogeneous structure of the greater portion of these processes, differing so markedly from the vacuolated granular protoplasm of the rest of the cell, is also more in accord with their being flagella, as pseudopodia have the same structure as the body of the cell from which they are protruded.

It is difficult to suggest the probable function of these giant flagella. They are evidently motile organs, as they may be found in all stages of flexion, some being practically straight, while others are bent almost into a semicircle. Their action probably serves to keep the liquid in the coelenteron in slow motion, thereby securing a more equal distribution of the nutrient substances contained therein to the cells in their vicinity.

Many of the endoderm cells are provided with "muscle processes," but these processes are not numerous in the pinnules and in the stem; they are more numerous in the endoderm of the tentacles and of the free portion of the polyp. The muscle-fibres (except those forming the retractors and protractors) have a circular direction, and are similar to those of *Alcyonium*. In *Alcyonium*, however, the endoderm cells of the tentacles do not possess muscle-fibres (Hickson, 1895, p. 376).

In teased preparations the muscle-fibres of the ordinary endoderm cells may be clearly seen (Fig. 26). On looking at the flagella-bearing cells in the same preparations, it is seen that most of these cells bear at their inner ends two processes which appear to be less stiff than the muscle-fibres of the ordinary endoderm cells, and which are never in a straight line with each other, but are invariably bent more or less towards each other (Fig. 27). It is possible that these are the modified muscle-fibres of the cell, as they appear to be homogeneous, and, when treated with fuchsin or iron hæmatoxylin, stain similarly to, though rather less deeply than, the muscle processes of ordinary endoderm cells. The bending inwards of the two processes from the inner end of the cell causes them to become rather more deeply embedded in the mesoglœa than the muscle processes of the ordinary endoderm cells, and the cell is therefore provided with a firmly fixed base upon which the giant flagellum can work as on a fulcrum.

It is worthy of note that throughout the whole of the colony the muscle processes of the endoderm cells (except the protractor and retractor muscles on the mesenteries) are circular in direction, whereas the similar processes (where present) of the ectoderm cells are longitudinal in direction.

Zooxanthellæ are exceedingly numerous in the endoderm of the pinnules, so numerous that, in many cases, the lumina of the pinnules are entirely closed. They are also numerous in the endoderm of the tentacles and of the free portion of the polyp, but in the cœlentera of the stem there are few, except near the upper end. There do not appear to be any large gaps between the endoderm cells in the lower parts of the cœlentera, as described by Hickson in *Alcyonium*, but the endoderm cells in this part are more or less spherical in shape, and are only loosely connected together.

MESOGLEA.

1. *Of the Free Portion of the Polyp.*—The mesoglœa of the body of the polyp varies in thickness from 0.02 mm. to 0.06 mm., while that of the tentacles is much thinner, averaging 0.013 mm. The mesoglœa of the pinnules is exceedingly thin, especially when they are expanded (cf. Figs. 11, 17).

Cells which connect the ectoderm and endoderm may be seen cross-

ing the mesogloea in all parts of the tentacles and body of the polyps. In the tentacles, however, these cells are few in number, but in the body of the polyp, where the mesogloea is thicker, the cells are more numerous. They are usually elongated or fusiform cells, having their outer ends embedded in or connected with the ectoderm, and their tapering inner ends passing into the endoderm (Fig. 17). In most cases the connection between the two cell-layers is established by means of a single cell, but in some cases two or more cells are placed end to end to form the connecting cord. In most cases the larger portion of the cell and its nucleus are situated in the ectoderm, and this, together with the nature of the cell, which closely resembles an ectoderm cell in appearance, points to the fact that these cells in the mesogloea are derived from the ectoderm. Besides these moderately large cells, the protoplasm of which is finely granular and often contains a few small vacuoles, there are other cells of very much smaller size which bear several or many processes. Some of the cells lie close to the ectoderm, while others are near the endoderm. They are connected together by their exceedingly slender processes, which traverse the mesogloea and unite with each other. These cells resemble, and are probably homologous with, the nerve-cells and nerve-fibres of *Alcyonium* and the *Actiniae*. They will be further described below (see p. 209). The mesogloea of the mesenteries and its included cells have already been described (see p. 197).

2. *Of the Stem* (see Pl. XX., Figs. 8 and 9).—On examining transverse sections of the upper portion of the stem there is seen a slightly denser ring of mesogloea (*Mg. D.*) around each of the coelentera. This ring of denser mesogloea is itself moderately free from cells, being crossed only at intervals by a cell or thin cord of cells, but it is bordered by an almost complete cordon of cells, interrupted only for the passage of endodermic canals. The canals of the stem are moderately large and very numerous, being much more highly developed than those of *Alcyonium*. The canals may be divided into the two systems described below.

The Superficial Canal System.—This system of canals is formed by numerous endodermic canals (*Sup. Can.*, Figs. 8 and 9) which are situated in the stem about .1 mm. beneath the ectoderm. This system

is really a fine network of numerous canals, which have a similar structure and appearance in all parts of the colony. The canals are about .08 mm. in diameter. In the intervals between these canals there are usually cords of ectoderm cells (*Ect. Str.*) which pass from the ectoderm to cells in the deeper parts of the mesogloea. In many cases the superficial endodermic canals are themselves closely connected with the ectoderm by strands of cells passing across the mesogloea from the ectoderm to the outer walls of the canal lying beneath. From the inner wall of these canals cords of cells frequently pass inward into the mesogloea, and are connected with other cells, with the coelentera, or with longitudinal canals.

The superficial canals are also present on the convex summit of the stem (see Fig. 8), and form there a plexus of canals, with similar relations to those above described in the cylindrical portion of the stem. In this portion of the stem the canals embrace or pass round each coelenteron at a distance of about .2 mm., and communicate by means of branches with the coelenteron and with the neighbouring longitudinal canals. The superficial canals on the convex summit are continuous at the edge of the summit with the corresponding canals of the cylindrical portion of the stem. In the stem the superficial canals frequently communicate with the neighbouring coelentera and longitudinal canals. Thus, by means of branch canals, this superficial system of canals is placed in communication with the remaining cavities lined by endoderm, and by means of strands of cells is placed in communication with the ectoderm and with the neighbouring cells in the mesogloea.

Where a stem divides there are extra canals which establish thorough communication between the superficial canals of the two branches.

As the base of the colony is approached there is a tendency for the superficial canals to send inwards wide branches, and in the lowest 2 mm. of the stem such branches are given off in large numbers, and unite with the complicated anastomosis of longitudinal canals present in that part of the stem.

This system of canals is of great importance, as all the young buds produced in the colony are formed by enlargement and growth outwards and inwards of one of these canals, the endoderm and lumen of the canal forming respectively the endoderm and coelenteron of the young polyp (see also p. 222).

Histology of the Superficial Endodermic Canals.—The endoderm lining the cavity of the superficial canals is always much thicker on the outer side of the canal than on the inner side (Pl. XXII., Fig. 29). This is caused by the cells on the outer sides being columnar and longer than the cubical or slightly flattened cells of the inner side of the canal.

The cells lining these canals resemble the endoderm cells of the cœlentera, but their protoplasm is somewhat less vacuolated, and therefore does not so markedly present the reticulate appearance which is so usual in the endoderm of the cœlentera. None of the cells of these canals bear flagella. Among the bases of the cells there are small cells which are probably stages in the formation of the larger ones. Some of the cells of the canals appear to be provided with very slender muscle processes. There are numerous zooxanthellæ in the lumen of the canals and embedded in the endoderm lining the cavity.

The Internal Canal System.—The canals forming the main portion of this system are chiefly longitudinal in direction, and commence in the umbrella-shaped portion at the top of each stem. Each canal runs in a sinuous or zigzag course in the mesoglœa, about equidistant from the surrounding cœlentera.

The longitudinal canal communicates with the superficial canals lying around its origin (Fig. 8). During its course down the stem the longitudinal canal very frequently communicates by small transverse canals with the neighbouring cœlentera and canals, and the longitudinal canals in the outer portion of the stem communicate also with the superficial canals. Owing to the frequent occurrence of branches, the longitudinal canals are nearly always angular in transverse section, one (or more) of the angles being usually produced into a small branch canal. The branch canals vary greatly in size; in the upper and middle portions of the colony being small, and their lumen very small or obliterated altogether, while near the base of the colony the branches are almost as large as the main canal. At the base of the colony these longitudinal canals give off several rather larger lateral branches on all sides, some of which unite with similar branches from adjacent canals, while others open into neighbouring cœlentera. Owing to the presence of so many canals in this region of the stem, the mesoglœa is penetrated in all directions by a complicated network of canals, which place all the cavities lined by endoderm in intimate communication

with each other. Very close to the base of attachment of the colony, a canal may usually be seen passing from each side of the lowest portion of each primary coelenteron, so that in longitudinal section the coelenteron and its two canals appear **┐**-shaped. The canal opens into the base of a neighbouring coelenteron. These canals are probably the representatives of the original stolon from which all the primary coelentera grow out.

The well-developed longitudinal canals running parallel to and between the coelentera of the polyps of *Xenia* remind one of the coenenchymal tubes of *Heliopora coerulea*, described by Moseley (1881) and by Bourne (1895). The resemblance is more striking when we consider that in both cases the longitudinal tubes are lined by endoderm, and are connected near the upper surface of the colony with a network of superficial endodermic canals.

The differences between the canals of *Xenia* and the coenenchymal tubes of *Heliopora* are chiefly due to the fact that in the latter only the outer portion of the coral is living, the internal parts consisting of calcareous skeleton only, whereas in *Xenia* the whole colony is penetrated by living cells. In *Heliopora*, therefore, the coelentera of the polyps and all canals running into the colony must terminate within about 2 mm. of the surface, as this is the lowest limit of the living substance. The coenenchymal tubes of *Heliopora* have an exactly similar course to the longitudinal canals of *Xenia*, as they run parallel to the coelentera from their point of origin from the superficial canal system (just beneath the ectoderm covering the free surface) to the base of the living portion of the colony, where they and the coelentera terminate blindly.

Moseley (1881) believed the coenenchymal tubes of *Heliopora* to be degenerate siphonozooids from which the mesenteries had disappeared, but Bourne (1895) has shown that they cannot be so regarded.

In order to find a parallel to these coenenchymal tubes of *Heliopora*, Bourne thought it necessary to go outside the *Alcyonaria* and compare the tubes with certain longitudinal canals of *Millepora*, described by Moseley (1876). After carefully studying the canal system of *Xenia*, it appears to me that this course is not now necessary, as the comparisons instituted above between the coenenchymal tubes of *Heliopora* and the longitudinal canals of *Xenia* are perfectly justifiable. It is true the coenenchymal tubes of *Heliopora* are more numerous than the longitu-

dinal canals of *Xenia*, but this also is probably due to the different modes of growth of the two corals. In *Heliopora* the living part is, as it were, spread out in a thin film, and the polyps are a considerable distance (1 mm. to 2 mm.) apart, several coenenchymal tubes being therefore required to place the coelentera in communication with the intervening ectoderm, calicoblasts (or skeleton-forming cells), and mesogloea. In *Xenia* each stem is an elongated, cylindrical, compact mass of living tissues, and the polyps are much closer together, the coelentera being only about .25 mm. to .4 mm. apart in the stem, and therefore one longitudinal canal, situated in the mesogloea between adjacent coelentera (together with the auxiliary strands and cords of cells which are so well developed in this *Xenia*), is sufficient to provide efficient communication between the coelentera and all parts of the narrow mesogloéal column between them.

Histology of the Longitudinal Endodermic Canals.—These canals are lined by a single layer of cells of equal thickness on all sides (cf. the superficial canals). The cells are more or less cubical in shape, and closely resemble the endoderm cells lining the coelentera. None of the cells in the canals bear flagella, but some bear slender muscle processes which, like those of the endoderm of the coelentera, are chiefly circular in direction. In the canals near the base of the colony many nematocysts, each in its cnidoblast cell, may be seen lying among the endoderm cells. In the upper portions of the colony nematocysts are seldom seen in the canals. Zooxanthellæ are present only in those longitudinal canals which are situated in the circumferential portions of the stem and in the upper portion of the canals, where they approach the summit of the stem.

Cells in the Mesogloea.—On examining a transverse section of the upper end of a stem of the colony, an almost complete chain of cells is seen surrounding the denser ring of mesogloea round each coelenteron (Fig. 9, *Ect. Ch.*). Each ring of cells is situated at a distance of about .06 mm. to .07 mm. from the endoderm of the coelenteron within. These cells are the ectoderm of the portion of the polyp enclosed in the stem, as can be seen on examining a longitudinal section through the upper part of the stem (see Fig. 8), when this cylinder of cells is seen to be continuous and in line with the ectoderm of the free portion of the

polyp. That these cells are ectodermic is further shown by the fact that spicules and nematocysts are found in them in moderate numbers, especially in the upper portion of the stem (Figs. 8 and 9, *Sp. Nem.*). Adjacent cylinders of cells are placed in intimate communication by numerous cords of cells which traverse the mesoglœa between them.

Sections taken further down the stem shew that the ring of cells becomes less complete and less definite, and each ring widens and recedes into the mesoglœa a little further from its cœlenteron. As they recede further and further, the rings of cells often coalesce in the mesoglœa at a point almost equi-distant from their cœlentera; and, as the longitudinal canals also lie in this region, the cells come to lie in relation with, and form a plexus around, the canals. There is, therefore, still a cylinder of cells round each cœlenteron, but the cylinder is not quite so regular as in the upper portions of the stem, being interrupted at frequent intervals, and is further away (.15 mm. to .2 mm.) from the enclosed cœlenteron.

In the upper portion of the stem the cylinder of cells has the same relation to the endoderm of the cœlenteron within it, as have the ectoderm and endoderm of the free portion of the polyp to each other. Crossing the denser ring of mesoglœa between the cylinder of cells and the endoderm are cells (viz. the vacuolated and granular cells, and the small nerve-cells) exactly like those observed in the mesoglœa of the free portion of the polyp.

Lower down the stem the cylinder of cells has been pressed further away from its cœlenteron, probably by the later growth of the mesoglœa, and is interrupted at intervals for the passage of canals and cords of cells which place all parts of the mesoglœa in intimate communication with the cœlentera, the canals, and the external ectoderm. Bourne (1895) has shown that in *Xenia umbellata* these rings of cells are ectodermic on account of their connection with, and general resemblance to, the ectoderm of the free part of the polyp, and the occurrence of spicules and nematocysts in some of them.

The cords of cells in the mesoglœa are then chiefly ectodermic, as they arise from the cylinders of cells around the cœlenteron, or, in the outer portion of the mesoglœa, migrate inwards from the inner irregular surface of the external ectoderm. The cells all present a similar appearance, being either rounded or rather elongated in shape, with somewhat vacuolated protoplasm. The elongated cells frequently

taper at their ends into long slender processes which become connected with similar processes of adjacent cells.

Some of the cords of cells are, however, obviously formed by obliteration of the lumen of a small canal; these cells are, of course, endoderm.

SPERMATOGENESIS (Pl. XXII., Figs. 30—35).

The specimen is a male, and shows beautifully all the stages in the development of the spermatozoa

Gonads are most numerous in the upper portion of the stems of the colony, but many sperm sacs are found in the basal part of the free portion of the polyps, and a few also in the lower portions of the colony. Sections through the upper portion of the stems show that sperm sacs are so numerous that they practically fill up the cavity of the coelentera of several of the older polyps (Pl. XX., Fig. 8, S. S.). In these cases most of the sperm sacs are no longer spherical, but by mutual pressure have become angular, being usually pentagonal or hexagonal in section.

The genital cells are derived from the cells which lie in the mesogloea of the mesenteries near their inner or free edge. These cells, as shown above (see p. 197), have migrated to their present position in the mesogloea from the endoderm, so that the gonads are, in this as in other *Alcyonaria*, endodermic in origin.

Each sperm sac originates as a slight projection at the side or free edge (except in the dorsal mesenteries) of the mesentery, and consists of one of these genital cells covered by a thin sheet of mesogloea, and by a single layer of endoderm cells continuous with the endoderm of the sides of the mesentery. The genital cell, the protoplasm of which is finely granular, or sometimes contains small vacuoles, is spherical and about .01 mm. in diameter, and in the centre has a large spherical nucleus whose diameter is about half that of the cell.

The nucleus and protoplasm of the genital cell undergo division, which at first is apparently regular, as many cases of four or eight cells so produced may be seen (Fig. 30). The divisions of the genital cell are accompanied by divisions of the endoderm cells covering it, and very soon the increase in size of the sperm sac causes it to project as a spherical or oval body from the mesentery, to which it always remains attached by a stalk consisting of a thin cord of mesogloea surrounded

by endoderm. When the sperm sac has reached a diameter of about .06 mm. to .08 mm. there appears in the centre a small cavity, free from nuclei, but containing some coagulable substance (Fig. 31, *Cg.*). This central cavity continues to enlarge for some time, along with the growth of the sperm sac (Fig. 32), and attains its maximum size in sacs about .2 mm. to .25 mm. in diameter, in which the central cavity reaches a diameter about one-fourth that of the sperm sac. After reaching this size it is gradually encroached upon by the heads of the ripening spermatozoa (Fig. 33, *Spz.*), and in the fully developed sperm sac, which is about .35 mm. in diameter, the cavity has completely disappeared, the whole of the interior of the sperm sac being filled with a mass of somewhat loosely packed spermatozoa, many hundreds in number, produced by the continued division of the single primitive genital cell. There are no examples of karyokinesis in the many hundreds of sperm sacs I have examined.

The head of each ripe spermatozoon (Fig. 34) consists of a blunt, conical, anterior piece fixed to the spherical nucleus. The length of the head is $7\ \mu$, the nuclear portion being $4\ \mu$ in diameter. The tail is a slender filament about $27\ \mu$ long.

The spermatozoa closely resemble those of *Alcyonium* in their structure and development (Hickson, 1895). The endoderm covering the sperm sac appears to undergo certain changes as the sperm sac grows, and in thin sections from two to five nuclei may be counted in many of the endoderm cells. One of these nuclei is sometimes larger than the others. In the left upper cell of Fig. 35 the large nucleus near the centre occupies the position of the original nucleus of the cell. The other four nuclei have probably been produced from it by division, but there has been no corresponding division of the protoplasm. The cell with four nuclei which was figured by Hickson (1895, Pl. 39, Fig. 45, f.) from the teased preparations of the sperm sacs of *Alcyonium*, was probably one of the cells of the endodermic follicle.

At first it appeared that the sperm sacs were situated on ventral and lateral mesenteries only, although, as pointed out above (see p. 197), the cells in the mesogloea, from which the genital cells are derived, are found in the dorsal mesenteries as well. After examining a large number of sections, I have found only two clear cases of sperm sacs occurring on the dorsal mesenteries. In each case the sperm sac is situated on the side of the mesentery a little distance from the free

edge, so that, although the sac is of considerable size (.15 mm. in diameter), it does not push the dorsal mesenterial filament out of position, and, judging from the sections, would not impede its action.

Empty sperm sacs the walls of which are collapsing may be seen in several sections. The spermatozoa are discharged into the coelenteron by bursting of the follicle of the sperm sac, and are then swept out to the exterior through the stomodæum. In sections of two polyps in which spermatozoa were escaping, the spermatozoa are found along the dorsal side of the stomodæum, being doubtless driven out by the upward or outward current produced by the cilia of the dorsal mesenterial filaments. Although escaping in a mass they are not enclosed in the follicle, but lie loosely aggregated in the dorsal position of the stomodæum. These two examples support the conclusion expressed above that the spermatozoa are discharged into the coelenteron by rupture of the follicle, the collapsed remains of which retain for some time their attachment to the mesentery.

As spermatozoa are present in all stages of development, it is likely that the discharge of ripe spermatozoa continues over a considerable period,—in fact, probably throughout the year. This is perhaps due to the fact that, living on reefs in the shallow waters of tropical seas, this coral is not subject to any great variations in temperature and food supply. In this respect *Xenia* differs from *Alcyonium digitatum*, which occurs in the colder seas of Northern Europe. In the latter all the sperm sacs of a colony have reached a similar stage of development and are all ripe about the same time of the year, viz. December, and therefore the discharge of ripe spermatozoa occurs only over a limited period, probably over about a month (Hickson, 1895).

NERVOUS SYSTEM.

In several sections there is a plexus of fine fibrils in the mesogloea connected with very small cells in relation with the ectoderm and endoderm. This plexus appears to be homologous with the similar plexus described by Hickson in *Alcyonium* (1895, p. 371), and compared by him to the "Nervenschicht" of the *Actinice*.

In this *Xenia* the plexus is best seen in sections of a polyp in which the ectoderm is cut slightly obliquely. On examining in such a section (Pl. XXI., Fig 16) the part where the ectoderm passes into the mesogloea, very fine fibrils (*N.F.*) may be seen, forming an open network,

upon which cells (*N.C.*) are situated at intervals. The fibrils can be best seen in the mesoglœa, but can be traced close to the ectoderm and endoderm. The cells of the nervous system are exceedingly small, and usually fusiform, triradiate, or stellate in shape, the angles of the cell being produced into nerve fibrils.

On tracing the fibrils outwards from the mesoglœa into the ectoderm, they are seen to be in connection with small cells which are situated in the deeper part of the ectoderm. Owing to the irregularity of the inner face of the ectoderm, and to the presence of spicules in the portion of the layer where the nerve-cells are situated, it is not possible to obtain a section which shows the ectodermic nerve plexus clearly, but small portions of it may be seen where the spicules are slightly less numerous.

In the case of the endodermic nerve plexus this difficulty does not exist, and an oblique section through the wall of a polyp shows that the plexus of fibrils in the mesoglœa is connected with minute stellate cells situated upon the outer face of the muscle processes of the endoderm cells. Hæmatoxylin (especially Heidenhain's iron hæmatoxylin and Meyer's acid hæmalum) stains the nerve-cells and fibres most clearly.

HISTORY OF OUR KNOWLEDGE OF THE BUDS OF THE XENIIDÆ.

Besides the fully developed polyps, the description and measurements of which are given above, there are on most of the branches of the colony young polyps or buds in various stages of development. These buds are invariably found at the edge of the umbrella-shaped area at the end of the stem. On one stem (Fig. 1, left) there are ten small buds varying in length from .5 mm. to 3 mm., and about fifty larger polyps from 5 mm. to 10 mm. in length. The smallest buds have simple tentacles devoid of pinnules, and all stages between these and the adult polyps may be found. As the polyps (both young and old) of *Xenia* are non-retractile, this genus offers considerable advantages for the study of the development of the polyps, and the young polyps have been noticed by many observers.

Quoy and Gaimard (1833) first observed these small polyps in the *Xeniidæ*. They noticed them in *Cornularia viridis*, which appears to belong to the genus *Xenia*, and they suggested that these small

polyps, the tentacles of which were devoid of pinnules, were young forms which had not yet attained the adult characters.

In 1874 Kölliker described *Heteroxenia Elizabethæ*, in which small individuals are very numerous. He regarded these small individuals as being of two kinds, some being young polyps in various stages of development, others being "zooids." *Heteroxenia*, therefore, is dimorphic. According to Kölliker, there are several essential differences between these two kinds of individuals.

I. *The Polyps*.—These are of large size, the adult measuring 20 mm. to 55 mm. in length, and about 3 mm. in breadth. There are also obviously younger polyps, 5 mm. to 20 mm. long, all of which are situated round the edge of the disc. The tentacles of the adult polyps bear two series (in each of which four rows are distinguishable at the base of the tentacles) of long cylindrical pinnules, one on each side of the middle line of the tentacle. The cœlentera of these polyps extend a considerable distance into the stem of the colony, and are crowded with ova.

II. *The Zooids*.—These are much more numerous than the polyps and much smaller, measuring only 3 mm. to 5 mm. in length and from .7 mm. to 1 mm. in breadth. The tentacles are eight short simple lobes, .14 mm. to .2 mm. in length, and they bear no pinnules. The cœlentera of these zooids extend at most only 3 mm. into the stem, and contain no gonads.

It should be noted that Kölliker saw two kinds of small individuals, and described the differences between them in size, structure, and position, viz.: (1) the young polyps, 5 mm. to 20 mm. long, found only round the edge of the disc; and (2) the "zooids," 3 mm. to 5 mm. long, found all over the disc among the bases of the large polyps.

Klunzinger (1877), who described the *Xeniidæ* of the Red Sea, saw small polyps in a specimen of *Xenia umbellata*; he called them bud-like polyps, and said that their tentacles which are at first simple, very soon show indentations or pinnules. He regarded such individuals rather as young polyps than as zooids. They were more numerous in the outer part of the arched end of the stem. In a new species *Xenia fuscescens*, Klunzinger described the small polyps as very numerous, outnumbering the large polyps, and filling up the intervals between the bases of the latter. He wrote that these small individuals do not

appear to develop into fully-formed polyps, but to remain in the bud-like stage, with short, simple, mostly incurled tentacles. They are 1 mm. to 2 mm. long and .5 mm. broad, and are cylindrical or club-shaped. On account of the large numbers of these small individuals, Klunzinger placed his *Xenia fuscescens* near the *Heteroxenia Elizabethæ* of Kölliker. There are no transition stages between these small individuals which do not appear to develop into larger polyps and the adult polyps, and from the description and figures they appear to be quite as distinct as the two kinds of individuals described by Kölliker in *Heteroxenia*.

Haacke (1887), who examined some of the *Xeniidæ* in Torres Straits, says that the small individuals are merely young polyps, and all stages of development between them and the adult polyps may be met with. Therefore he denies the occurrence of heteromorphism in the *Xeniidæ*.

Wright and Studer in the 'Challenger Report' (1889) record the observations of Klunzinger and Haacke noticed above. They agree with Haacke, and therefore propose the provisional abandonment of Kölliker's genus *Heteroxenia*.

Bourne (1895) observed in his new species, *Xenia Garciaæ*, numerous imperfect polyps or buds in all stages of growth at the edge of the polyp-bearing summits of the stems. He remarked that "these are not siphonozooids, but stunted or developing polyps."

Bourne also described a specimen which he referred provisionally (being unable to procure Kölliker's original description) to the species *Heteroxenia Elizabethæ*. In his description were noted:—

(1) The larger polyps with well-developed tentacles, with three rows of lateral pinnules on their margins, their cœlentera continued to the bottom of the stem or nearly so, and filled with ova. At the edges of the arched end of the stem there were numerous young polyps in all stages of development, many of which showed distinct pinnules on their tentacles.

(2) Closely applied sterile zooids which have no tentacles, but only eight radiate lobes round the mouth. The cœlentera of these individuals extend only a little way into the stem, and then communicate with the cœlentera of the polyps by anastomosing endodermic canals. Among these zooids there are never any individuals which show signs of pinnate tentacles nor which contain gonads. Bourne concludes that in this form there is distinct dimorphism.

Schenk (1896) mentions the occurrence of buds in eight new species of *Xenia* from Ternate, which he has described. He briefly describes the external characters of the buds in *Xenia viridis*, and figures three stages of development. The first figure represents a small bud about 3 mm. long, in which the tentacles are simple finger-shaped lobes. The other two are drawings of slightly larger polyps the tentacles of which bear, in one case six, and in the other about twelve pinnules on each side of the tentacle (seen from the outer side). In all the examples mentioned by Schenk the small individuals are young polyps in course of development, as pinnules have already appeared on the tentacles of many of them. Schenk (*loc. cit.*, p. 53) remarks that he believes the zooids of K  lliker are merely young polyps, and therefore *Heteroxenia Elizabeth  * does not exhibit dimorphism; hence he renames it *Xenia Elizabeth  *, and places it near *X. fuscescens*, Klunzinger. Thus Schenk supports Haacke's view that there is no dimorphism of the polyps of *Xenia*.

From this short account of previous observations it will be seen that the nature of these small individuals in the *Xeniidae* is not yet determined. That they are all buds or young polyps is strongly affirmed by Klunzinger, Haacke, Wright and Studer, and Schenk; while the opinion of K  lliker and Bourne is that they are of two kinds, some being young polyps and others quite different individuals, termed zooids.

With a view to coming to some definite conclusion regarding the nature of these small individuals, I have examined them in the specimen of *Xenia Hicksoni* in great detail. I have also examined the sixteen other specimens of *Xenia* at my disposal, and a specimen of the *Heteroxenia* which Bourne has described and figured. These will be briefly described below.

EXTERNAL CHARACTERS OF THE BUDS OF XENIA HICKSONI.

In *Xenia Hicksoni* the small individuals are all buds or young polyps, as in this one specimen every stage in development may be seen, from the youngest polyp only .32 mm. in length to the large adult polyp 12 mm. long; and the series is perfectly complete, there being no break at any point which would justify the division of the individuals into two kinds.

The buds are invariably found on the edge of the arched end of the stem. Their numbers vary on different stems, there being usually from six to ten buds less than 3 mm. long on each stem (Pl. XVIII., Fig. 1, left). The smallest bud (Pl. XIX., Figs. 4, 4A) measures .32 mm. in length and .44 mm. in width. It is situated just under the edge of the umbellate summit of the stem. It is a short cylindrical outgrowth, at the distal end of which the developing tentacles are indicated as eight small rounded lobes about .1 mm. long, divided from each other by shallow furrows. A slight depression in the centre of the distal end indicates the position of the future mouth, which is not yet open to the exterior. The tentacles increase in length rather more rapidly proportionately than the body of the polyp. In the smallest specimen they are less than one-third the total length of the polyp, but in rather larger polyps they form from two-fifths to one-half the total length of the polyp. The tentacles remain simple lobes until the polyps attain a length of nearly 1 mm. In a specimen .95 mm. long (Fig. 5) the tentacles have reached a length of .34 mm., and the tip of each tentacle is distinctly trilobed when seen from the outer side, *i.e.*, there is an indication of the formation of the first two pinnules, one on each side of the axis of the tentacle.

From this point onwards the formation of pinnules takes place regularly as the tentacles increase in size, as may be seen from the table below. When the polyp (Fig. 6) has reached a length of 1.42 mm. the tentacles, which are .6 mm. long, are seen from the outer aspect to bear four pinnules on each side. If one of the tentacles be examined from the inner side it will be seen that an inner row of pinnules has already been formed (Fig. 6A). The polyp from which Fig. 7 was drawn was 2.27 mm. long, and its tentacles 1.30 mm. long. Seen from the outer aspect the tentacles show eight pinnules on each side. For a distance of about two-thirds of a millimetre from the tip of the tentacle, there are on the inner face two rows of pinnules on each side of the middle line, but a little nearer the base of the tentacles the three rows of pinnules on each side, characteristic of the tentacles of the adult, may be seen (Fig. 7A).

After the earliest stages of growth are passed the polyps grow quite regularly, and the length of the tentacles bears to the total length of the polyp an almost constant proportion. From the appended table of measurements it will be seen the tentacles form rather more than

two-fifths of the whole length of the polyp. With the increase in length of the tentacles there is a corresponding increase in the number of pinnules which the tentacles bear, and, as the following table shows, there is a perfect series of examples, beginning with the very young specimens, in which the tentacles are devoid of pinnules, and ending with the largest polyps, whose tentacles show from the outer aspect nineteen or twenty pinnules on each side of the middle line. The gradual transition from the youngest to the oldest polyps shows that the small individuals in this colony are undoubtedly young buds in various stages of development. They are all "polyps," using the word in the sense in which it was used by Kölliker.

Reference Number.	Total length of Polyp (Body and Tentacles).	Width of Polyp.	Length of Tentacles.	Number of Pinnules on each side of Tentacle (outer aspect).	
	mm.	mm.	mm.		
I.	.32	.44	.10		Pl. XIX., Figs. 4, 4A.
II.	.43	.4	.12	0	In sect., Pl. XXII., Fig. 28.
III.	.56	.37	.19	0	—
IV.	.8	.4	.31	trace of first	—
V.	.95	.35	.34	Trilobed=1	Pl. XIX., Fig. 5.
VI.	1.0	.34	.43	Trilobed=1	In section, Pl. XX., Fig. 8.
VII.	1.1	.5	.53	2	—
VIII.	1.42	.87	.6	4	Pl. XIX., Figs. 6, 6A.
IX.	1.6	.96	.7	4—5	—
X.	2.0	.86	.86	6	—
XI.	2.1	.8	1.03	7	—
XII.	2.27	.6	1.3	8	Pl. XIX., Figs. 7, 7A.
XIII.	2.8	.86	1.4	8	—
XIV.	3.2	.9	1.4	8—9	—
XV.	4.0	1.0	1.8	10	—
XVI.	6.1	.9	2.4	10—11	—
XVII.	6.5	.9	2.5	11—12	—
XVIII.	6.8	1.1	2.85	13	—
XIX.	9.1	1.2	4.2	14—15	—
XX.	12.0	1.2	5.1	17	—
XXI.	11.65	1.2	5.7	19—20	Pl. XIX., Fig. 2.

I find in all the sixteen other specimens of *Xenia* at my disposal, young buds in all stages of growth, similar to those described and figured in *Xenia Hicksoni*. Most of these young buds occur on the arched end of the stem, but in two of the colonies examined a few buds are found in the middle portion of the summit between the bases of the larger polyps. These buds, however, differ in no way from those round the edge of the summit.

EXTERNAL CHARACTERS OF *HETEROXENIA ELIZABETHÆ*.

(Pl. XXII., Fig. 37).

Bourne (1895) has already described the external characters of a colony similar to this one, but a brief description will be given here. The colony is somewhat triangular in shape, the base of the triangle being formed by the polyp-bearing summit of the stem. The stem is slightly flattened, and is narrow at its lower end, gradually widening from below upwards. The total length of the stem is about 30 mm., its breadth at the base 12 mm. by 6.5 mm., its breadth at the top 23 mm. by 6 mm.

The non-retractile polyps (4) are long and slender, and measure on an average about 15 mm. in length (including the tentacles), though a few specimens reach almost 30 mm. in length. The polyps are 1 mm. to 2 mm. broad. The tentacles of the polyps measure 4 mm. to 5 mm. in length, and bear on the inner side two series of rather slender pinnules, each series consisting of three rows of about sixteen to twenty-four pinnules in each row. In one or two of the tentacles examined, the pinnules at the base are so arranged that it is difficult to say whether they are in three or four rows on each side of the middle line. The pinnules in the middle of the tentacle measure about .5 mm. in length, and are about four times as long as they are broad. The middle line of the tentacle is free from pinnules along the greater part of its length. The polyps are 1 mm. to 3 mm. apart, but they are closer together round the edge of the summit of the stem than on the middle portion of the summit. Around the edge of the summit of the stem there are many small polyps in all stages of development,—in fact, all the polyps near the edge of the summit are small ones, the large ones being situated in the middle portion of the polyp-bearing area.

The walls of the polyps are thin, and when the colony is removed from spirit the polyps fall together and form a confused mass on the end of the stem.

Between the bases of the polyps there are many closely apposed small zooids (Fig. 37, S.), quite different in appearance from buds or young polyps. The siphonozooids, are from six to ten times as numerous as the polyps or autozooids, and they occur all over the summit of the stem. The siphonozooids are all similar in appearance, being

cylindrical or club-shaped, 2 mm. to 5 mm. in length and .5 mm. to 1 mm. in diameter. The tentacles are eight small rounded lobes arranged round the mouth; they are never longer than .25 mm., and never possess pinnules.

Bourne provisionally referred this specimen to K  lliker's species *Heteroxenia Elizabethae*, and, after comparing the specimen with K  lliker's original account and figures (1874), I can confirm his conclusion. This specimen is much smaller than K  lliker's, its polyps being only about half the size, but there are many points of agreement between them, viz. general anatomy and proportion of parts, size, and structure of zooids; size, colour, and distribution of spicules; canals, &c.

After carefully examining the two kinds of small individuals (viz. young polyps and zooids), I have no doubt that they are entirely different in nature. The external characters are quite different, and there are important differences in their internal arrangements, to which reference will be made.

External Characters of the Young Polyps of Heteroxenia Elizabethae.—The youngest polyp, which is also by far the smallest individual on the colony, is .64 mm. in length (Fig. 38). Its tentacles are finger-shaped lobes .24 mm. to .3 mm. in length. The tip of one of the tentacles is slightly three-lobed, but all the other tentacles have simple rounded ends.

A polyp 1.4 mm. long, the tentacles of which have attained a length of .4 mm., are trilobed at their ends, *i.e.*, the first pinnule on each side of the axis is being formed. The formation of pinnules proceeds regularly with the growth in length of the tentacles, and the adult size and characters are gradually attained. From the appended table it will be seen that there is a complete series of stages from the smallest polyp, .64 mm. long, with simple tentacles devoid of pinnules, to the largest polyp, nearly 30 mm. long, the tentacles of which show on the outer face twenty-four pinnules on each side of the middle line. In this *Heteroxenia* the ratio between the length of the tentacles and the total length of polyp is not quite as constant as in the *Xenia* considered above. The tentacles form about one-fourth to one-third the length of the whole polyp.

MEASUREMENTS OF THE AUTOZOIDS OF *HETEROXENIA ELIZABETHÆ*.

Reference Number.	Total Length of Polyp.	Width of Polyp.	Length of Tentacles.	Number of Pinnules on each side of Tentacle (outer aspect).	
	mm.	mm.	mm.		
A 1 . . .	·64	·3	·24—·3	0—1	Pl. XXII., Fig. 38.
A 2 . . .	1·4	·5	·4	Trilobed=1	—
A 3 . . .	2·0	·7	·9	3—4	A 3, Fig. 37.
A 4 . . .	2·8	·9	1·0	5	—
A 5 . . .	4·4	·7	1·3	7	A 5, Fig. 37.
A 6 . . .	5·8	1·1	1·7	8	—
A 7 . . .	6·0	1·1	2·2	12—13	—
A 8 . . .	9·1	2·0	3·1	15	—
A 9 . . .	12·8	1·2	3·5	15—16	—
A 10 . . .	14·0	2·4	4·3	16	—
A 11 . . .	20·2	2·0	5·0	18	—
A 12 . . .	28·4	2·4	5·2	24—25	—

External Characters of the Siphonozooids of Heteroxenia Elizabethæ.—The siphonozooids, like the autozooids, are non-retractile. These vary in length from 1·8 mm. to 5·0 mm., and are ·5 mm. to 1·0 mm. wide. Their tentacles are all in the same condition, and are mere lobes from ·2 mm. to ·25 mm. in length, and never show any traces of the formation of pinnules. It will be seen from the appended table that there is no development of the tentacles corresponding to the increase in length of the individuals, so that the tentacles of a zooid 5 mm. in length are very similar to those of a specimen less than half its size (compare S 1 and S 7 in table).

TABLE OF MEASUREMENTS OF THE SIPHONZOZOIDS OF *HETEROXENIA ELIZABETHÆ*.

Reference Number.	Total length of Zooid.	Width of Zooid.	Length of Tentacles.	
	mm.	mm.	mm.	
S 1 - - -	1·8	·7	·2	—
S 2 - - -	2·0	·8	·2	—
S 3 - - -	2·3	·8	·23	—
S 4 - - -	3·0	·8	·24	—
S 5 - - -	4·5	1·0	·2	—
S 6 - - -	4·8	·6	·25	—
S 7 - - -	5·0	·8	·2	Figs. 37, 39.
S 8 - - -	5·0	·9	·25	—

By means of their rudimentary, short, rounded tentacles the zooids may be readily distinguished from young polyps of the same size, whose tentacles are longer, pointed, and bear pinnules. Compare, for example, the young polyp A 5 (see table, p. 218) with the siphonozooid S 5. They are both about the same length, but the tentacles of the former are 1.3 mm. long, and, examined from outer aspect, show seven pinnules on each side of the middle line, whereas the tentacles of the siphonozooid are only .2 mm. long, and are simply rounded lobes. Now if, as urged by Schenk and others, these two individuals are both young polyps, how can the differences in the size and character of their tentacles be accounted for? If the zooids are stages in the development of polyps, it is very difficult to account for so many being in the same stage of development (as the tentacles of all the specimens examined are in the same simple condition), when, on the same colony, other individuals of the same length, or even smaller, have already acquired some of the adult characters, viz., the pinnate tentacles. On the colony drawn in Fig. 37 there are over two hundred zooids, all of which are similar in appearance, having simple round tentacles. The examples indicated in the above table are chosen haphazard from this large number, being arranged in order of length merely for convenience of reference. If these were young polyps we should expect to find a more or less constant increase in the length of, and alteration in the character of, the tentacles, with the increase in length of the individuals; but this is not the case. We should also expect them to resemble other individuals of the same length on the colony which are undoubtedly young polyps; but, as we have seen, they are very different.

It must be concluded, then, that these zooids are different in nature from young polyps, and that there are in *Heteroxenia* two kinds of individuals, polyps and zooids, or, to use Moseley's terms, autozooids and siphonozooids.

THE INTERNAL ANATOMY OF *HETEROXENIA ELIZABETHÆ*.

Owing to the very imperfect preservation of the specimen, it is impossible to give a detailed account of the internal structure of the colony, and therefore attention will be chiefly directed to the points in which *Heteroxenia* differs from the *Xenia* described in detail in the former part of this paper.

Autozooids.—Spicules are numerous in the ectoderm of all parts of the body of the autozoid, and are very numerous in the ectoderm of the outer face of the tentacles. They are also present in the pinnales. They are similar in size and shape to those of *Xenia Hicksoni*. They are whitish or bluish white by reflected light, but of a reddish-brown tinge by transmitted light. Nematocysts are exceedingly scarce and difficult to find. They measure $9\ \mu$ in length and $2\frac{1}{2}\ \mu$ in width. The ectodermic muscles of the tentacles are well developed; the muscle band of the oral face is very much thicker than that of the aboral face.

The oral disc of each polyp is slightly contracted, producing a funnel-shaped depression leading to the mouth. The stomodæum is only 1 mm. to 1.5 mm. long, and is wrinkled or folded transversely. It bears a ventral groove or siphonoglyph, the cells of the lower half of which bear moderately long flagella. There are the usual eight mesenteries, bearing rather feebly developed retractor muscles on their ventral faces. Only the dorsal mesenteries bear mesenterial filaments, and these have a typical course and structure. Owing to imperfect preservation it is impossible to say anything definite about the cells of the other mesenteries, but no ventral or lateral mesenterial filaments are visible.

The coelentera of the polyps may be traced a considerable distance into the stem, those of the primary polyps being continued down to the base of the colony. In the upper portion of the stem the coelentera contain many ova, each of which is surrounded by an endodermic follicle attached to the mesenteries. The largest of these ova measure .3 mm. to .4 mm. in diameter.

Siphonozooids (Fig. 39).—Spicules are not so numerous in the ectoderm of the zooids as in that of the polyps.

The stomodæum is very badly preserved in most of the specimens. A few of the zooids situated near the edge of the summit, however, are rather better preserved, and two of these (S 3 and S 7 in the table, p. 218) have been sectioned and the stomodæum examined. In the zooid 2.3 mm. long the stomodæum measures .6 mm., and shows a well-marked siphonoglyph, the cells of the lower .2 mm. of which bear flagella. The other specimen (S 7 in table, see also Fig. 39) is 5 mm. long. Its stomodæum measures .8 mm. long, and the cells of the lower .4 mm. of the siphonoglyph bear flagella.

Thus both autozooids and siphonozooids of this specimen possess a

siphonoglyph, the cells of the lower half or third of which bear flagella. This does not agree with the observations of Hickson (1883, p. 696), on a specimen of *Heteroxenia*, in the siphonozooids of which he found a well-marked siphonoglyph, but in the autozooids a complete absence of siphonoglyph.

The siphonozooids possess the usual eight mesenteries, but they are extremely thin, and retractor muscles are not visible upon them. The dorsal mesenteries bear mesenterial filaments (Fig. 39, *D.M.F.*), which run in a sinuous course down the dorsal side of the polyp, and a short distance into the portion of the coelenteron contained in the stem. The coelentera of these siphonozooids cannot be traced more than two millimetres into the stem. At this depth the coelentera terminate in connection with one or more of the numerous endodermic canals. Ova are not present in any of these coelentera.

Stem.—No definite superficial endodermic canal system is distinguishable on the summit of the stem, except at its edge, where the young buds appear to originate from it. It is, however, present in the cylindrical portion of the stem, and has a similar appearance and relations to the corresponding canal system of *Xenia Hicksoni*.

The longitudinal canals are developed to a much less extent than in *Xenia Hicksoni*. They are small, and their lumen is often almost obliterated. Canals are most numerous in the upper part of the stem, especially in and immediately below the portion penetrated by the coelentera of the siphonozooids. In this region of the stem there are very numerous short transverse canals which place the various coelentera in intimate communication with each other.

THE ORIGIN AND INTERNAL STRUCTURE OF THE BUDS OF *XENIA HICKSONI*.

In this specimen the buds or young polyps arise on or just under the edge of the umbrella-shaped area at the end of the stem. In most other species of *Xenia* the buds generally arise in a similar position, but in two of the colonies I have examined, and in three of the new species described by Schenk (1896), buds occur not only round the edge, but a few also on the middle portion of the expanded end of the stem. The buds are much more numerous on the edge of the summit of the stem and in *Xenia Hicksoni*, and, in fact, in most specimens the buds are found only in this position.

On examining a transverse section of the upper portion of a stem of the colony, the cœlentera in the peripheral portion of the stem are seen to be smaller than those in the central portion, and some of them are obviously the cœlentera of very young polyps (Pl. XX., Fig. 9, right).

1. The buds arise in connection with that portion of the superficial endodermic canal system situated at the edge of the summit of the stem. When a bud is about to be formed, the superficial canal becomes enlarged and the outer wall of the canal becomes pushed outwards towards the surface of the stem. This produces a small tubercle upon or immediately under the edge of the expanded end of the stem. The tubercle increases in size, and its distal end soon becomes divided into eight small pouches which become the tentacles of the polyp (Pl. XIX., Fig. 4). The divisions between the pouches are the mesenteries of the polyp, and they gradually grow inwards into the cœlenteron. The eight mesenteries are already formed in the young polyp shown in Fig. 4.

In the centre of the free end of the bud there is a slight depression, and a small darker area which marks the position of the future mouth (Fig. 4 *Mo.*), and also the ingrowing plug of ectoderm which forms the stomodæum. Sections of this bud show that the stomodæum is .14 mm. long, and rather flattened laterally. Its oral end is still solid, but the inner portion has become tubular, and its cavity opens into the cœlenteron of the polyp. The distance from the depression indicating the position of the mouth to the innermost portion of the cœlenteron is .4 mm. Mesenteries are distinguishable only in the upper three-fifths of the cœlenteron. In other respects this polyp resembles the one described below, and drawn in Fig. 28.

2. A slightly older polyp (No. II. in table, p. 215, and drawn in section, Fig. 28), .43 mm. long, possesses tentacles which are not all of the same size. The dorsal and ventral ones are largest (about .12 mm. long), the two lateral ones a little smaller, and the remaining four still smaller. These differences in size are very well seen in transverse sections through the polyp at the level of the mouth. A second specimen of the same size was cut longitudinally, and shows several interesting points (Fig. 28). The stomodæum is about .32 mm. long, and is tubular along the greater part of its length. The mouth is, however, closed partly by approximation of the walls of the stomodæum and partly by a small plug of mucus. The

siphonoglyph is not yet differentiated. The distance from the mouth to the inner end of the coelenteron is about .7 mm. The mesenteries may be traced almost to the inner end of the coelenteron, and their retractor muscles are just distinguishable. The dorsal mesenteries are slightly thicker than the others, but their mesenterial filaments have not yet been formed. The coelenteron is formed by enlargement of the superficial endodermic canal. An evagination of the outer wall of the canal forms the coelenteron of the free portion of the polyp, and pushes outwards the mesogloea and ectoderm, thus giving rise to the protuberance which forms the free portion of the young polyp. A diverticulum produced by the bulging inwards into the mesogloea of the inner wall of the canal forms the inner part of the coelenteron.

The endoderm of the outer wall of the superficial canal is much thicker than that of the inner wall (Fig. 29). This difference enables one to see in section (Fig. 28) that the endoderm of the whole of the free portion of the polyp is derived from the thick outer wall of the canal. The endoderm of the portion of the coelenteron situated in the outer part of the stem is formed directly from that of the canal, while the endoderm of the inner portion of the coelenteron is derived from that of the thin inner wall of the canal, which has grown inwards into the mesogloea. The coelenteron gives off a large canal at its base, which opens into the adjacent longitudinal canals. During its short course in the stem the coelenteron communicates several times by means of short canals with the neighbouring superficial and longitudinal canals.

Among the endoderm cells of the middle portion of the coelenteron there are a very few flagella-bearing cells. The flagellum is a short conical or finger-shaped process which in these sections is never more than $15\ \mu$ in length.

3. A slightly longer bud (No. III. in the table, p. 215), .56 mm. long, possesses, like the preceding example, tentacles of different sizes. In this specimen also the dorsal and ventral tentacles are largest, the lateral ones being next in point of size, and the four intermediate ones somewhat smaller. Does this indicate the order of development of the tentacles? This bud resembles the preceding one in all essential particulars.

4. There are several important new structures noticeable in a young polyp .8 mm. in length (No. IV. in table, p. 215). The tentacles are

very slightly indented a short distance from the tip; this is the first indication of the formation of pinnules upon the tentacles.

The stomodæum is .57 mm. long, and oval in transverse section. It is open throughout its whole length, thus placing the cœlenteron in communication with the exterior. There is now also a marked ventral groove, which, however, is not distinguishable in the outer third of the stomodæum. The cells of the lower two thirds of the groove bear flagella, except for a very short distance near the inner end. Some of the cells of the lower half of the stomodæum contain a large cavity, and are similar to the goblet-cells described in the stomodæum of the adult. They are more numerous on the lateral walls of the stomodæum, and do not occur among the cells forming the siphonoglyph. The ectodermic muscles of the tentacles and the retractor muscles on the mesenteries are now quite obvious. The endoderm covering the mesenteries and lining the body-wall is very thick in the free portion of the polyp, (as in Fig. 28), and the inter-mesenterial spaces are consequently very small. The mesenteries may be traced nearly to the end of the cœlenteron, *i.e.*, about 1 mm. below the lower end of the stomodæum. Flagella-bearing cells are present in the middle and lower portions of the cœlenteron, but the flagella are still few in number and of small size, never exceeding $20\ \mu$ in length.

The most novel feature in this polyp is the presence of dorsal mesenterial filaments, which may be traced more than halfway (.6 mm.) down the free edge of the dorsal mesenteries. They have already acquired their typical structure, *i.e.* each is a band of ciliated cells on the somewhat thickened edge of each of the dorsal mesenteries, and there is a longitudinal groove down the middle of the band, so that in transverse section it is V-shaped. The filaments have a very sinuous course, and are therefore cut across two or three times each in the same section. These filaments are undoubtedly derived from the lower end of the stomodæum, with which they are perfectly continuous. Their cells are exactly like the cells of the stomodæum, being small and having homogeneous or finely granular deeply staining protoplasm and dark nuclei. Their cells differ markedly from the cells of the surrounding endoderm, which are larger, have reticulate protoplasm, stain more lightly, and have less distinct nuclei.

There is another very interesting feature worthy of note in this

polyp, viz., that sexual cells are already clearly differentiated. Sections through the mesenteries in the lower part of the coelenteron show that a considerable number of the endoderm cells covering the mesenteries are more spherical, and two or three times as large as their neighbours. They have clearer protoplasm than the ordinary endoderm cells, and their nuclei are large ($5\ \mu$ in diameter) and vesicular, and possess a well-marked, deeply staining nucleolus (Fig. 36 shows them in a slightly older polyp). These cells occur in all the mesenteries, but are more numerous in the ventral and lateral than in the dorsal ones. Some of the cells have already migrated into the mesogloea of the mesenteries, but most of them still retain their position in the endoderm. These modified cells are present only in the portion of the mesenteries situated in the lower two-thirds of the coelenteron.

On comparing these cells with the primitive sperm cells of the adult the resemblance is so striking that I am convinced these modified endoderm cells are the sexual cells which have become differentiated at this early stage in the development of the polyp. This view is supported by the following facts :

a. They are at first endoderm cells covering the mesenteries, which, on becoming differentiated, migrate into the mesogloal lamina of the mesentery. This agrees with the origin, migration, and position of the sexual cells traced in the adult polyps (see p. 197).

b. These cells are found in the mesenteries some distance below the lower end of the stomodæum. They are not present in the mesenteries of the free portion of the polyp, but in the portion enclosed in the stem. They are therefore in the position in which the genital products of the adult polyps are most numerous (see p. 207, and Fig. 8).

(c) They agree in size and are similar (especially their large vesicular nuclei) in appearance to the primitive genital cells of the adult.

Fig. 36 shows a section through a ventral mesentery of a slightly older polyp (No. V. in table, p. 215). The genital cells are still more clearly marked than in the preceding polyp, and, as shown in the figure, are readily distinguished by their large vesicular nuclei. Many of them have already taken up their position in the mesogloea.

On comparing the polyp $\cdot 8$ mm. long with one about two-thirds its size ($\cdot 56$ mm. long) it is seen that during the period in which the elongation of $\cdot 24$ mm. was accomplished, many important adult structures were acquired, viz., the first indication of pinnules on the

tentacles, the open mouth, the siphonoglyph, the goblet-cells in the stomodæum, the dorsal mesenterial filaments, and the primitive genital cells. A polyp which has reached this stage of development would probably be quite capable of supporting itself, as, by means of its siphonoglyph and dorsal mesenterial filaments, it would be able to create the currents necessary for its nutrition and for keeping up the circulation of liquid in the cœlenteron.

In a polyp .95 mm. long (V. in table, p. 215) the first two pinnules are distinguishable upon each tentacle. The stomodæum is .6 mm. long, and the siphonoglyph extends along the ventral side of the lower, .34 mm. The lips of the stomodæum are widely open below. Flagella-bearing cells are much more numerous in this polyp than in any of the young polyps previously described. They are fewer in number in the upper part of the cœlenteron than in the deeper portions. Their flagella are still short, not exceeding $30\ \mu$ in length (Fig. 36, *G. F.*).

A polyp 1 mm. long (VI. in table) is seen in section in Pl. 25, Fig. 8. Its tentacles bear near the tip one pinnule on each side of the axis. The stomodæum is .74 mm. long, and exhibits a well-marked siphonoglyph, bearing flagella in its lower half. The dorsal mesenterial filaments are well developed, and extend in a sinuous course nearly 1 mm. down the cœlenteron. The cœlenteron extends 1.4 mm. into the stem, curving so as to be parallel to the neighbouring cœlentera. Its connections with the longitudinal and superficial canals may be seen in the figure. The flagella of the endoderm cells attain $40\ \mu$ in length. The distribution of spicules, nematocysts, and zooxanthellæ is shown in the figure. In such a polyp all the adult structures are differentiated. In the growth of the polyp, from this point onwards to the full adult size, there are few features which call for comment. The chief of these are the formation of a greater number of pinnules on the tentacles; the elongation of the cœlenteron outwards (as the free portion of the polyp grows in length) and inwards into the mesogloea, where it curves, so as to lie parallel to the neighbouring cœlentera (Pl. 25, Fig. 8); the increase in number and size of the giant flagella on the endoderm cells, and the development of sperm sacs on the mesenteries.

GENERAL SUMMARY.

The following is a recapitulation of the new points to which reference is made (paragraphs 1, 2, and 6 have been already published in 'Proc. Roy. Soc.,' 1898):

1. The absence of ventral and lateral mesenterial filaments usually present in the polyps of the *Aleyonaria*. The only previously recorded examples of the absence of these filaments are the siphonozooids which occur in some other *Aleyonacea* and in Pennatulids.

2. The absence of these filaments is correlated with the presence of gland cells in the stomodæum, which occur especially in the ventro-lateral walls which abut on the siphonoglyph. Their position is suggestive of the digestive function of the cells, as their secretion can be readily poured out on to the ingoing food particles.

3. The non-retractile nature of the bodies of the polyps and of the stems is accounted for by the absence of muscle-fibres from their ectoderm cells, and by the presence of numerous spicules in these parts. The presence of ectodermic muscles in the tentacles, pinnules, and distal millimetre of the bodies of the polyps, together with the absence of spicules from these parts, confers the power of contractility, slight though it is, upon these parts. The muscle processes of the ectoderm cells (where present) are longitudinal in direction, while those of the endoderm cells are circular (except the protractor and retractor muscles on the mesenteries).

4. Nematocysts were found in *Sarcophyton*.

5. An extraordinary number of spicules is present in the basal part of the colony, and much of the mesogloea is converted into a dense horny substance. Thus a firm base of attachment is provided which would afford a rigid support for the branches which arise from it.

6. Many of the endoderm cells lining the coelentera and tentacles bear giant flagella, which may attain $120\ \mu$ in length.

7. In adult polyps the primitive genital cells are formed by differentiation of some of the endoderm cells which cover the mesenteries. These genital cells migrate into the mesogloea of the mesenteries, and then move outwards, one at a time, each cell pushing the endoderm and a thin film of mesogloea before it, and so forming a small tubercle on the side or end of the mesentery. By division of the genital cell the spermatozoa are produced. They remain until ripe, surrounded by

a thin film of mesogloea, and by a layer of endoderm cells, many of which contain from two to five nuclei.

8. The longitudinal canals which traverse the mesogloea of the stem are very well developed, and are physiologically, and possibly morphologically, equivalent to the coenenchymal tubes of *Heliopora cœrulea*.

9. The nervous system is similar to that of *Alcyonium*; the stellate cells immediately outside the endodermic muscle-fibres are very clearly seen.

10. A complete series of developing polyps is described, beginning with very young specimens, in which the tentacles are devoid of pinnules, and ending with the adult polyps with multi-pinnuled tentacles.

11. A similar series of polyps of *Heteroxenia Elizabethæ* is described and compared with the siphonozooids of the same colony. It is concluded that *Heteroxenia* is undoubtedly dimorphic, as stated by Kölliker and Bourne.

12. The origin of the buds of *Xenia Hicksoni* from the superficial canal system, their subsequent growth, and the appearance in them of the mouth, stomodæum, siphonoglyph, gland cells in stomodæum, mesenteries, dorsal mesenterial filaments, and flagella of the endoderm cells are traced. It is remarkable that the sexual cells are already differentiated in a young polyp .95 mm. long.

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EXPLANATION OF PLATES XVIII.—XXII.

Illustrating Dr. J. H. Ashworth's paper on “The Structure of *Xenia Hicksoni*, nov. sp. with some Observations on *Heteroxenia Elizabethæ*, Kölliker.”

LIST OF REFERENCE LETTERS.

A, A3, A5. Autozooids of *Heteroxenia* (the numbers refer to the table on p. 218). *Cg.* Coagulum in central cavity of sperm sac. *Cn.C.* Cnidoblast cell. *D.M.* Dorsal mesentery. *D.M.F.* Dorsal mesenterial filament. *Ect.* Ectoderm. *Ect. Ch.* Chain or cylinder of ectoderm cells round cylinder of denser mesogloea. *Ect. Str.* Strands of ectoderm cells. *End.* Endoderm. *End. Can.* Endodermic canals. *F.* Flagella of siphonoglyph. *G.C.* Gland-cells in stomodæum. *G.F.* Giant flagella of endoderm cells. *Gen. C.* Genital cells in various stages of development. *Long. Can.* Longitudinal endodermic canals. *L.M.* Lateral mesentery. *M.* Mesentery. *Mg.* Mesogloea. *Mg.D.* Denser cylinder of mesogloea around each coelenteron in stem. *Mo.* Mouth. *Muc.C.* Mucus cells of ectoderm. *M.P.* Muscle processes of endoderm cells. *N.* Nucleus. *Nem.* Nematocysts. *N.C.* Nerve Cells. *N.F.* Nerve fibrils. *R.M.* Retractor muscles in mesenteries. *S. S7.* Siphonozooids of *Heteroxenia* (the number refers to the table on p. 218). *Sec.* Secretion of gland-cells of stomodæum. *Si.* Siphonoglyph. *Sp.* Spicules. *Spz.* Spermatozoa. *St.* Stomodæum. *Sup. Can.* Superficial canal. *S.S.* Sperm sacs. *V.M.* Ventral mesentery. *Z.* Zooxanthellæ.

PLATE XVIII.

FIG. 1.—View of the colony of *Xenia Hicksoni*. From one of the stems on the left side all the larger polyps have been removed, so that the umbellate summit of the stem, with the young polyps growing round its edge, may be

more clearly seen. Note also that the polyps are smaller and closer together near the edge than nearer the middle of the summit. The stem immediately to the right of this also shows that the young and small polyps are on the edge, while the large polyps are near the middle of the summit. The colour of the drawing is, as nearly as possible, the colour of the specimen in spirit. $\times 3$.

PLATE XIX.

FIG. 2.—View of the polyp XXI. in the table, p. 215. This is one of the largest polyps of the colony. The tentacles show from the outer aspect a single row of pinnules on each side, but from the inner aspect three rows on each side. Note that at the tip of the tentacles the pinnules are *not* arranged in pairs. $\times 12$.

FIG. 3.—Views of the tentacle of a large polyp. *A* and *B* are views of the tip, *C* and *D* of the base of a tentacle. *A* and *C* show the outer or aboral side, *B* and *D* the inner or oral side. The narrow area free from pinnules, which extends along the middle line of the oral face of the tentacle, is well seen in *D*. At the tip of the tentacle, *B*, the pinnules are in two rows only on each side of the middle line. $\times 24$.

FIG. 4.—Lateral view of the youngest polyp (·32 mm. long) in the colony (I. in table). $\times 40$.

FIG. 4A.—Oral view of the same polyp. The tentacles are eight rounded lobes. The depression (*Mo.*) in the centre of the oral disc indicates the position of the future mouth, and the darker area below it is the ingrowing plug of ectoderm which forms the stomodæum. $\times 40$.

FIG. 5.—An older polyp 95 mm. long (V. in table). The tentacles are trilobed at the end, *i.e.*, the first pinnules are being formed. $\times 24$.

FIG. 6.—A polyp 1·42 mm. long (VIII. in table). $\times 24$.

FIG. 6A.—View of the oral face of a tentacle of the polyp shown in Fig. 6. Two rows of pinnules on each side of the middle line are now present. $\times 24$.

FIG. 7.—A polyp 2·27 mm. long (XII. in table). $\times 24$.

FIG. 7A.—View of the oral face of a tentacle of the polyp shown in Fig. 7. In the middle part of the tentacle, three rows of pinnules on each side of the middle line are now distinguishable. $\times 24$.

PLATE XX.

FIG. 8.—A thick longitudinal section through the upper part of one of the stems. The section passes along the dorso-ventral axis of a young polyp (VI. in table, p. 215) growing out just under the arched summit of the stem. On the dorsal or upper side of the polyp one of the dorsal mesenteries (*D.M.*) is cut through obliquely for a short distance. The stomodæum (*St.*), siphonoglyph (*Si.*), the course of the dorsal mesenterial filaments (*D.M.F.*), the thin edge of the ventral mesentery (*V.M.*), and the connection of the cœlenteron with the canal system are shown. Three cœlentera of older polyps are also shown.

Two of them are crowded with sperm sacs (*S.S.*), many of which, owing to mutual pressure, have lost their original spherical shape and are pentagonal or hexagonal in section. The other coelenteron contained a similar number of sperm sacs, but they have been omitted in order to more clearly show the dorsal mesenterial filament (*D.M.F.*) and the thin edge of the ventral mesentery (*V.M.*). The superficial (*Sup. Can.*) and longitudinal (*Long. Can.*) canal systems, and their relation to each other and to the coelentera; the denser cylinder of mesogloea (*Mg. D.*) with its surrounding ectoderm cells enclosing each coelenteron; and the distribution of spicules, nematocysts, and zooxanthellæ are also shown. $\times 35$.

FIG. 9.—A thinner transverse section through the upper part of one of the stems. The coelentera in the peripheral part are smaller than those nearer the centre. The coelenteron of a very young polyp is seen on the right. The cells in the mesogloea of the mesenteries and sperm sacs in various stages of development, attached to the mesenteries of the older coelentera, are also shown. The number of flagella cut across in one section is seen; thus an idea may be formed of their abundance and of their size relative to the endoderm and to the coelentera. Many of the features to which attention was drawn in the description of the previous figure are also shown here. $\times 50$.

FIG. 10.—Transverse section through a polyp at the level of the lower third of the stomodæum. The chief features shown are the gland-cells and siphonoglyph of the stomodæum, the somewhat feebly developed retractor muscles on the mesenteries, and the distribution of the spicules, nematocysts, and zooxanthellæ. $\times 50$.

FIG. 11.—Transverse section of the outer wall of a pinnule showing the ectoderm containing nematocysts, the mesogloea, and the endoderm cells with their reticulate protoplasm. $\times 800$.

FIG. 12.—A nematocyst in its cnidoblast cell, from a section. One half of each coil of the thread in the upper part of the nematocyst was cut away in sectioning. $\times 2000$.

FIG. 13.—Eight large spicules selected from those in the base of the colony. Each spicule is situated in a small cavity in the mesogloea. The nucleus and remains of the protoplasm of the spicule forming cell are seen. From sections. $\times 800$.

FIG. 14.—A portion of the outer part of the mesogloea from a transverse section of a polyp. Four of the spicules present their edge and two their flat face to the observer. $\times 800$.

FIG. 15.—Two very young spicules in their respective cells. The spicule in *A* is $3\frac{1}{2} \mu$ long and $2\frac{1}{2} \mu$ broad. The spicule in *B* presents its edge to the observer. It is 7μ long and $1\frac{1}{2} \mu$ thick. $\times 1000$.

PLATE XXI.

FIG. 16.—Section of the wall of a polyp which has passed very obliquely through the mesogloea, to show the nervous system. Five nerve fibrils in the mesogloea are connected on the outer side with cells in the outer part of the

mesogloea, some of which send processes into the ectoderm. On the inner side, the fibrils pass into small stellate nerve-cells situated just outside the muscle processes of the endoderm cells. $\times 300$.

FIG. 17.—Longitudinal section through the body wall of a polyp, to show the general character of the ectoderm and endoderm cells, and also the processes of ectoderm cells which penetrate the mesogloea and establish connection with the endoderm. $\times 400$.

FIG. 18.—Longitudinal section of the ventro-lateral portion of the lower third of the stomodæum. The chief feature shown is the large gland-cells, some of which have discharged their contents and appear empty, while others are in the act of discharging their secretion. $\times 600$.

FIG. 19.—Transverse section on the end of a dorsal mesentery showing the V-shaped mesenterial filament bearing cilia. $\times 600$.

FIG. 20.—Transverse section of the end of a ventro-lateral mesentery to show the general character of the endoderm cells, the giant flagellum of one of them, and the cells in the mesogloea. $\times 600$.

FIG. 21.—Transverse section of the end of the same mesentery taken .25 mm. higher, showing three flagella occurring close together. $\times 600$.

FIGS. 22, 23, 24.—Three flagella from sections of polyps to show their various degrees of flexion. $\times 600$.

FIG. 25.—Two abnormal forms of flagella from sections. *A* from the tentacle of a polyp, *B* from the portion of a cœlenteron in a stem. $\times 600$.

FIG. 26.—Endodermic myo-epithelial cells from teased preparations. In connection with the one on the right there is a small stellate cell with three long processes. This is probably one of the nerve-cells of the endodermic portion of the nerve plexus. $\times 500$.

FIG. 27.—Isolated cells bearing flagella, from teased preparations. $\times 500$.

PLATE XXII.

FIG. 28.—Section of a stem at the edge of the umbellate summit, to show the formation of a young polyp .43 mm. long (II. in table, p. 215). Note that the endoderm of the free portion of the polyp is thick, while that of the inner part of the cœlenteron is thin. The neighbouring cœlentera are cut very obliquely. $\times 50$.

FIG. 29.—The superficial canal indicated by the asterisk in Fig. 9 enlarged. The cells of the outer wall are longer and more columnar than those of the inner wall. $\times 500$.

FIG. 30.—Thin transverse section (3μ thick) of the end of a ventro-lateral mesentery, to which three very young sperm sacs are attached. In the one to the right the primitive genital cell has divided into four, three only of which are visible. $\times 500$.

FIG. 31.—Section of a sperm sac a little older than the largest one shown in the preceding figure. The central cavity containing a coagulum has now appeared. $\times 150$.

FIG. 32.—Section of an older sperm sac. $\times 150$.

FIG. 33.—Section of a mesentery, on the end of which is a sperm sac in which the central cavity, having reached its greatest size, is now being encroached upon by the heads of ripening spermatozoa. Note that the spermatozoa are surrounded by a thin film of mesogloea (represented in the distal part of the sac by the line inside the endoderm), and by an endodermic follicle, some of the cells of which contain from two to five nuclei. $\times 150$.

FIG. 34.—Ripe spermatozoa.

FIG. 34A.—From a section of the stomodæum, through the dorsal portion of which spermatozoa are escaping. Only the head and point of attachment of the tail are seen. $\times 800$.

FIG. 34B.—An entire ripe spermatozoon from a teased preparation of a large sperm sac. $\times 800$.

FIG. 35.—Cells from thin sections ($4\ \mu$ thick) of large sperm sacs, to show the two to five nuclei which may be present in each. $\times 800$.

FIG. 36.—Transverse section of a ventral mesentery of a young polyp .95 mm. long (V. in table, p. 215; see also Pl. 24, fig. 5). The section is taken about .5 mm. below the lower end of the stomodæum. Note the already differentiated primitive genital cells migrating from the endoderm into the mesogloea, and the short finger-shaped flagella of three of the endoderm cells. $\times 500$.

FIG. 37.—View of a colony of *Heteroxenia Elizabethæ*. The colony was split in two longitudinally and the proximal half drawn, hence only half the summit of the stem is seen. Note the autozooids with pinnate tentacles, and the very numerous short siphonozooids with short rounded tentacles, and also the young polyps growing near the edge of the summit. $\times 3$.

FIG. 38.—View of the youngest autozooid on the colony, .64 mm. long (Δ 1 in table, p. 218). The specimen has been flattened out by pressure against the side of the bottle which contained the colony. Note the long finger-shaped tentacles; the right proximal one is slightly indented near the tip, but the others have simple rounded ends. The stomodæum is indicated. $\times 40$.

FIG. 39.—The largest siphonozooid on the colony (S 7, Fig. 38, and table, p. 218). The short simple tentacles, the stomodæum, and the two dorsal mesenteries with their filaments are shown. $\times 15$.





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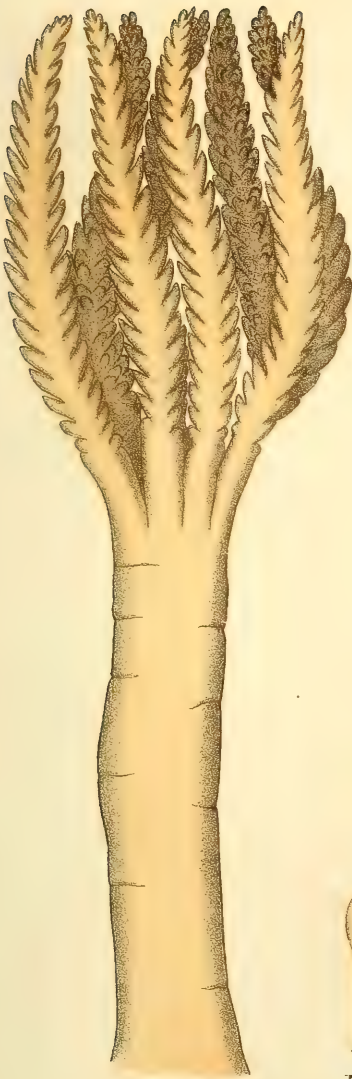


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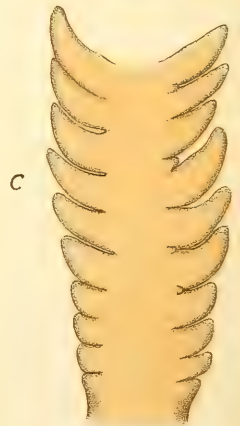
B



A



D



C

Fig. 3.



Fig. 5.

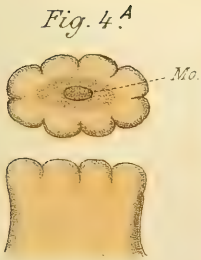


Fig. 4.^A

Fig. 4.



Fig. 6.



Fig. 7.^A



Fig. 6.^A

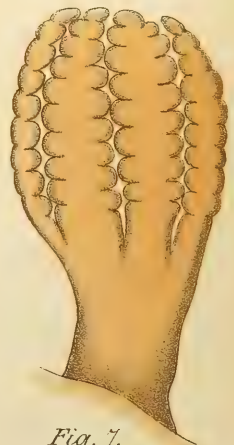


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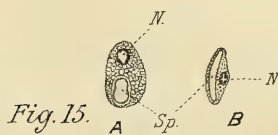
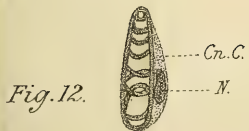
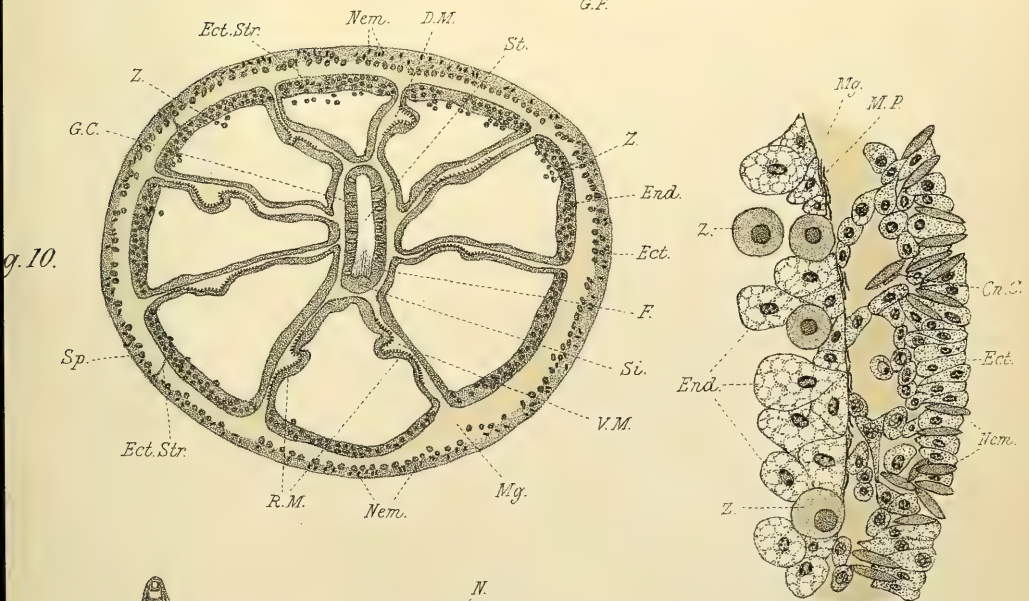
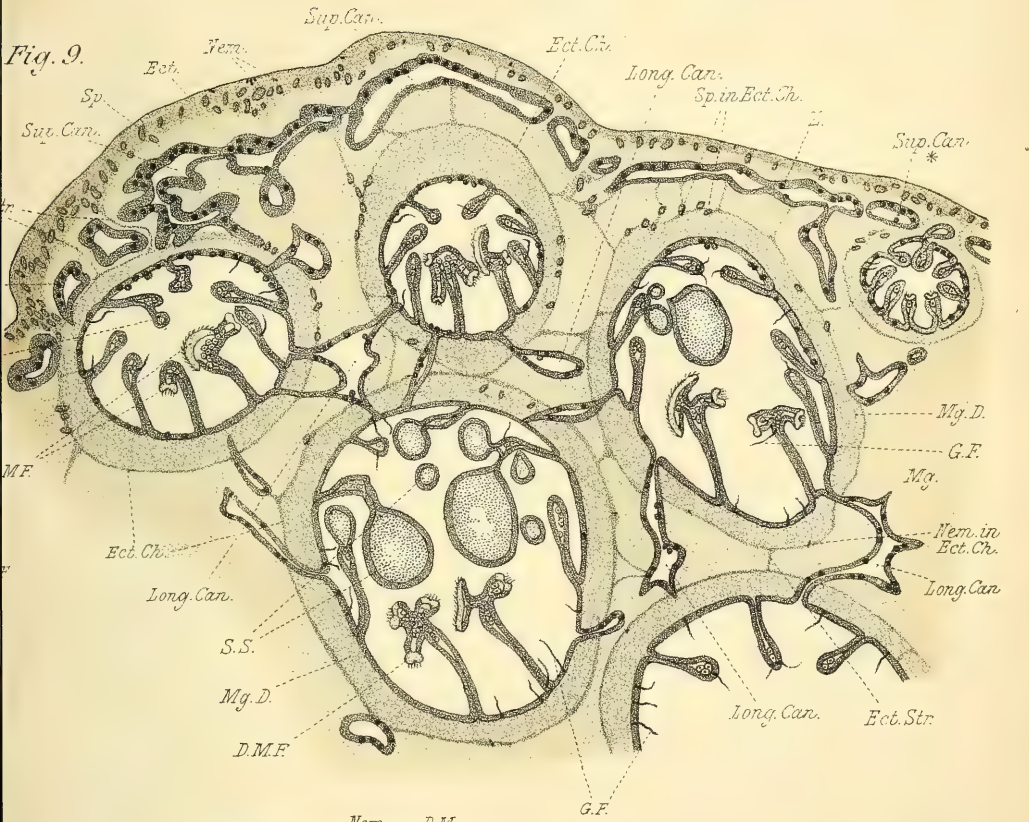
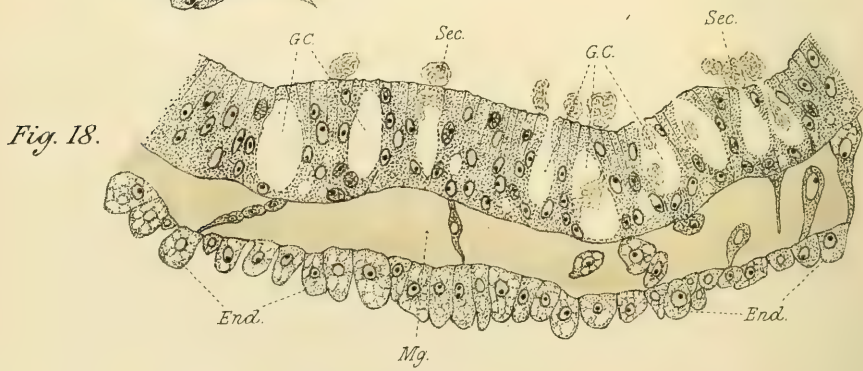
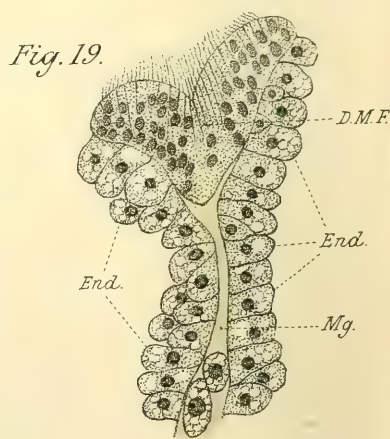
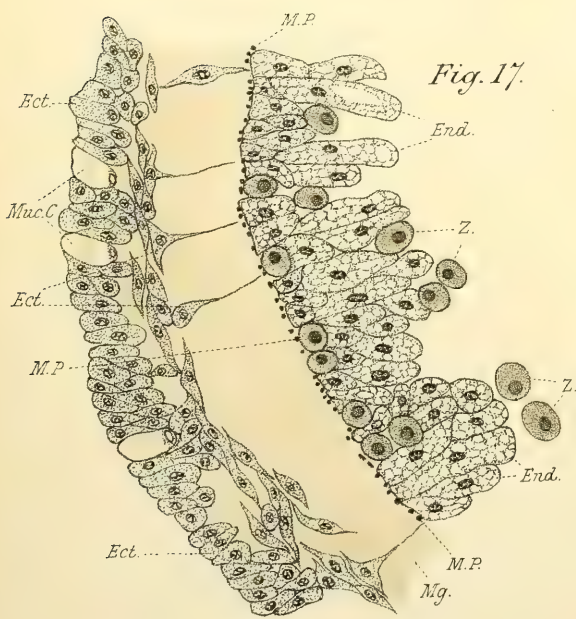


Fig. 11.



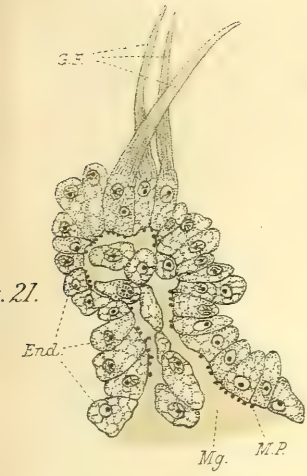


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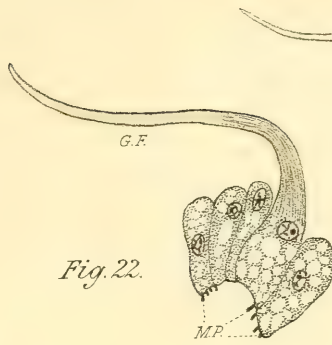


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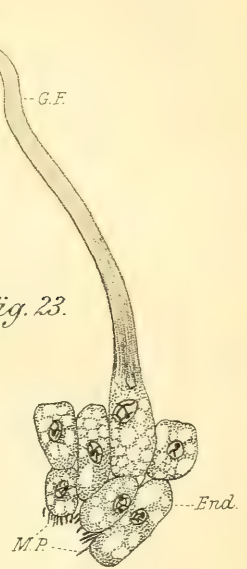


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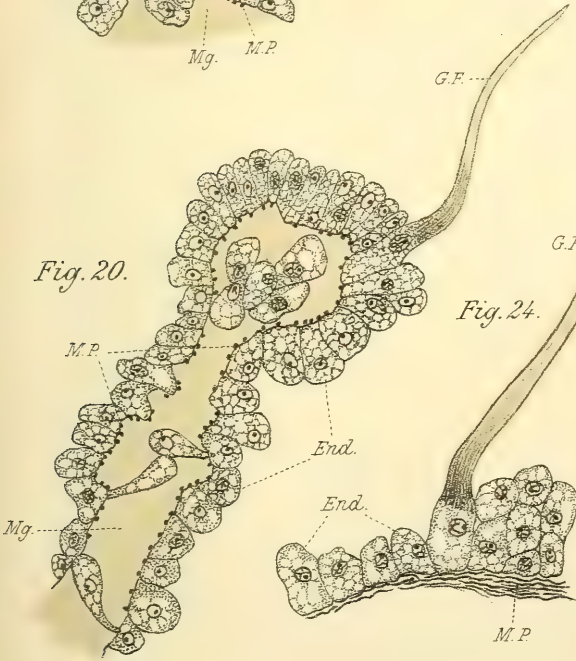


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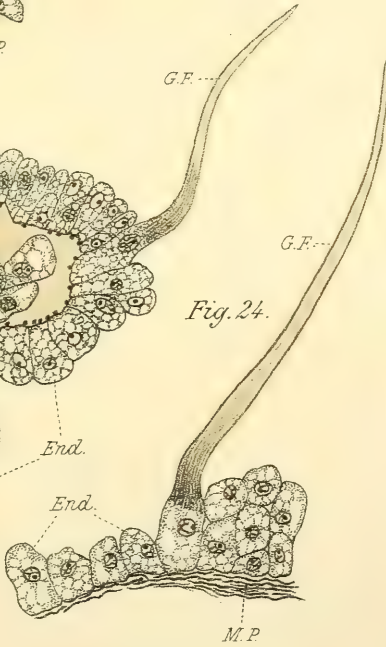


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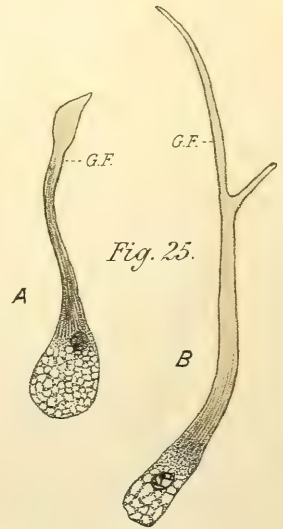


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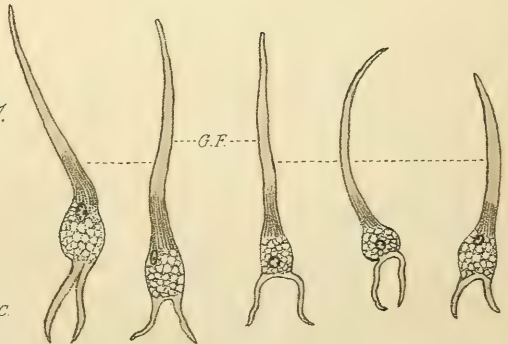
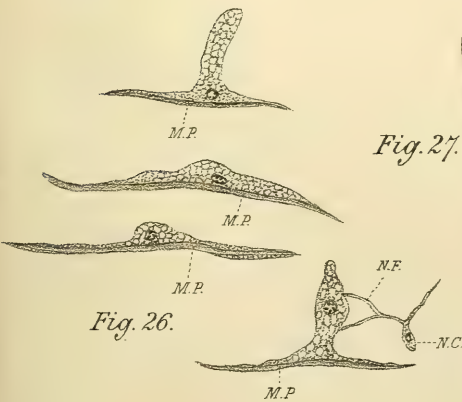


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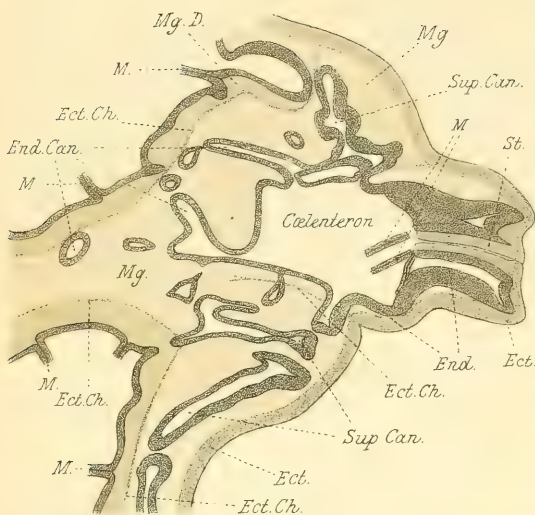


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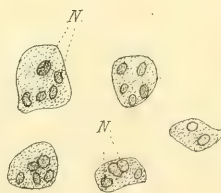


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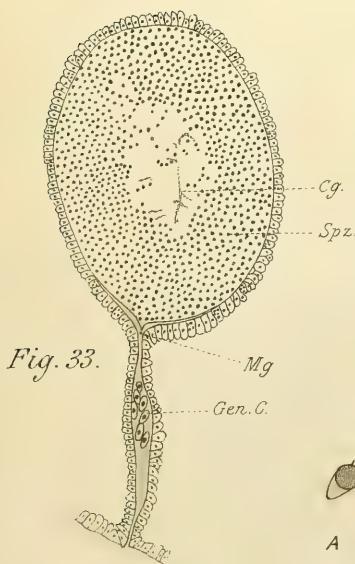


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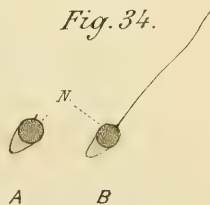


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Fig. 29.

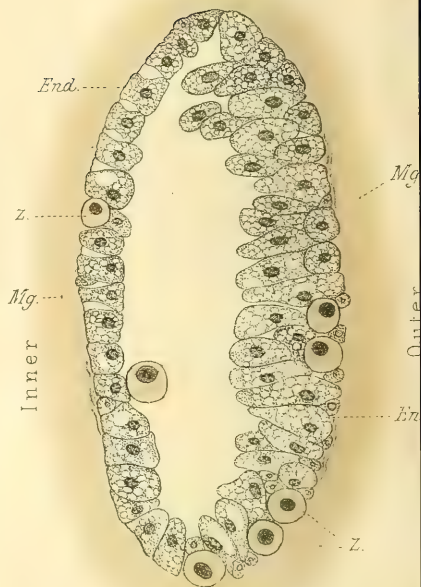
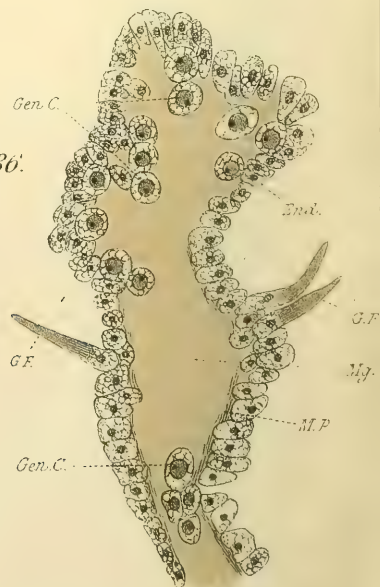


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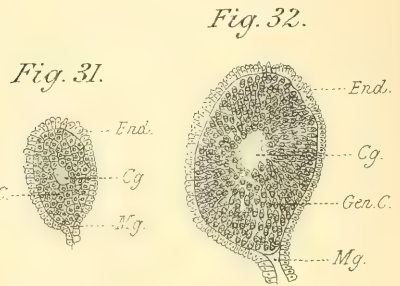
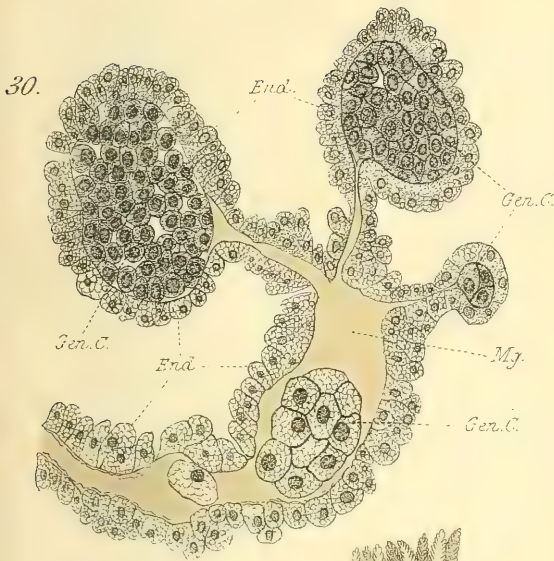


Fig. 32.

Fig. 37.

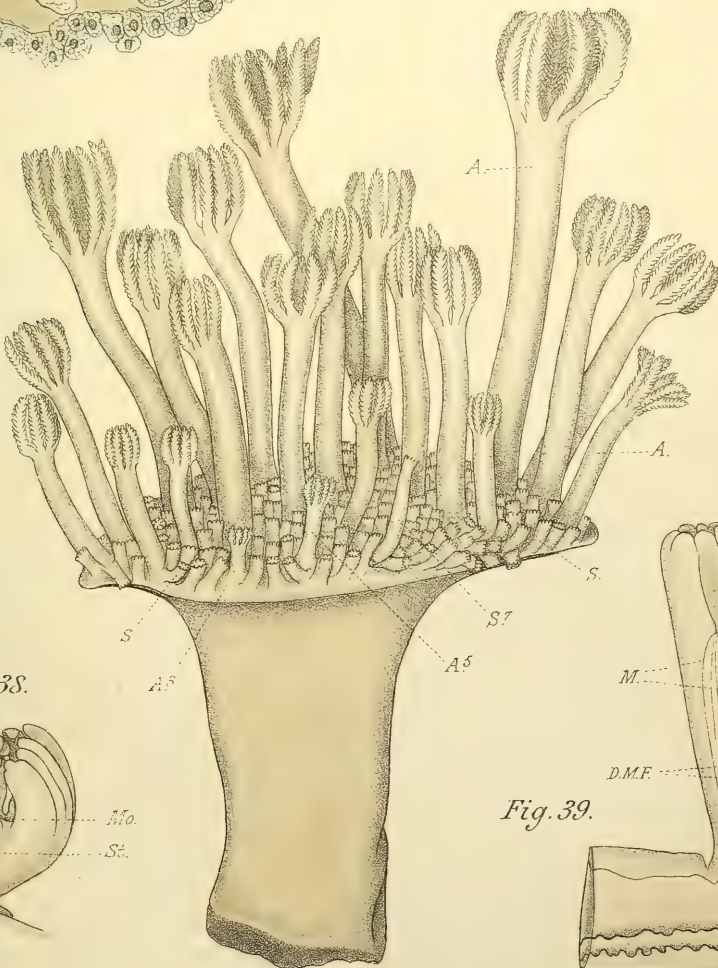


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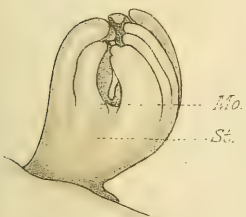
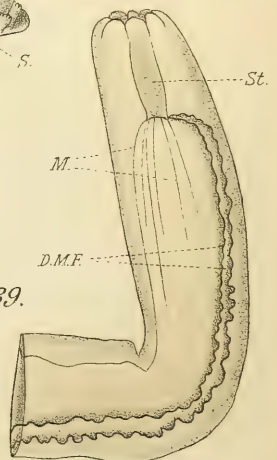


Fig. 39.



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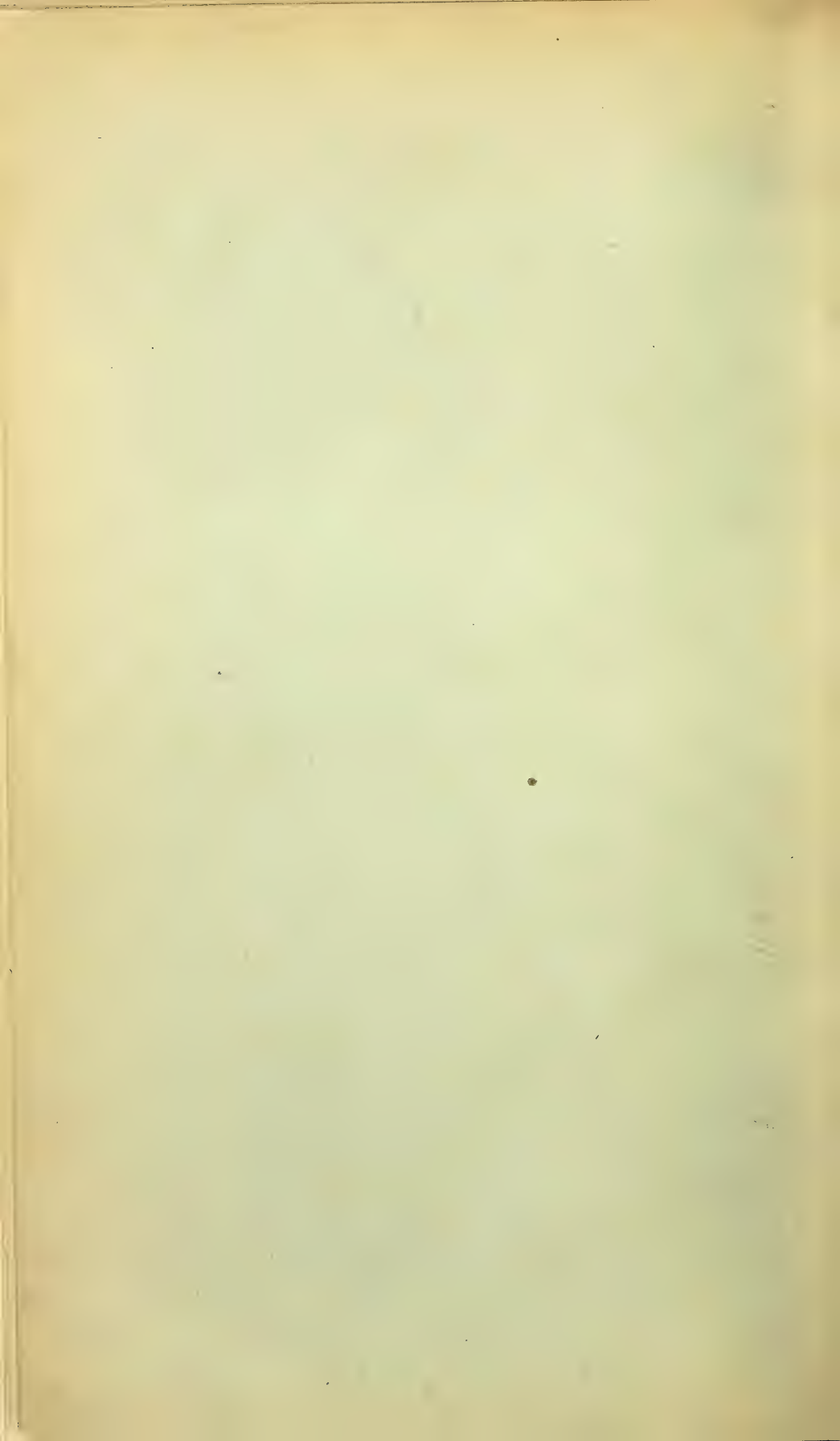
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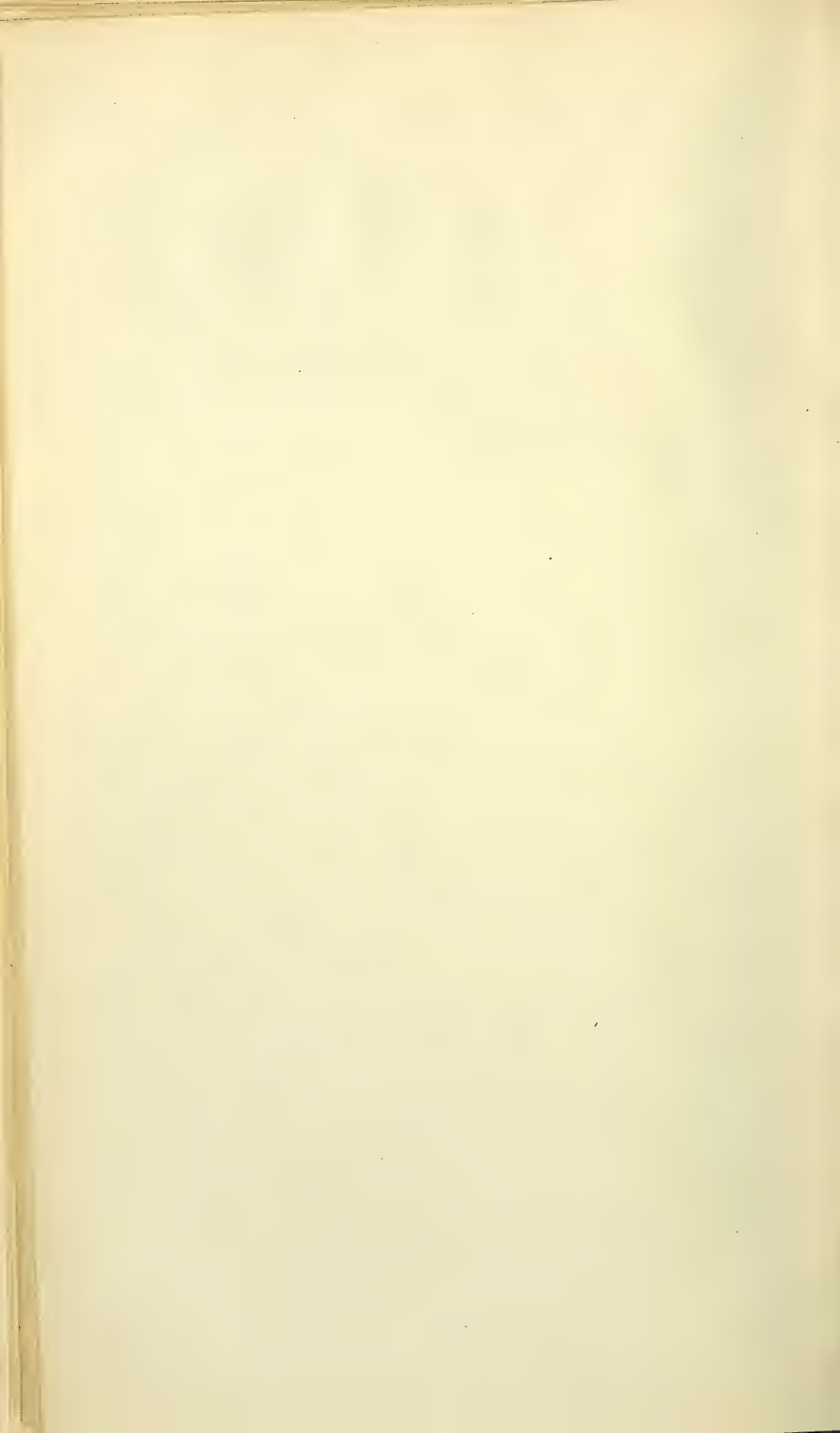
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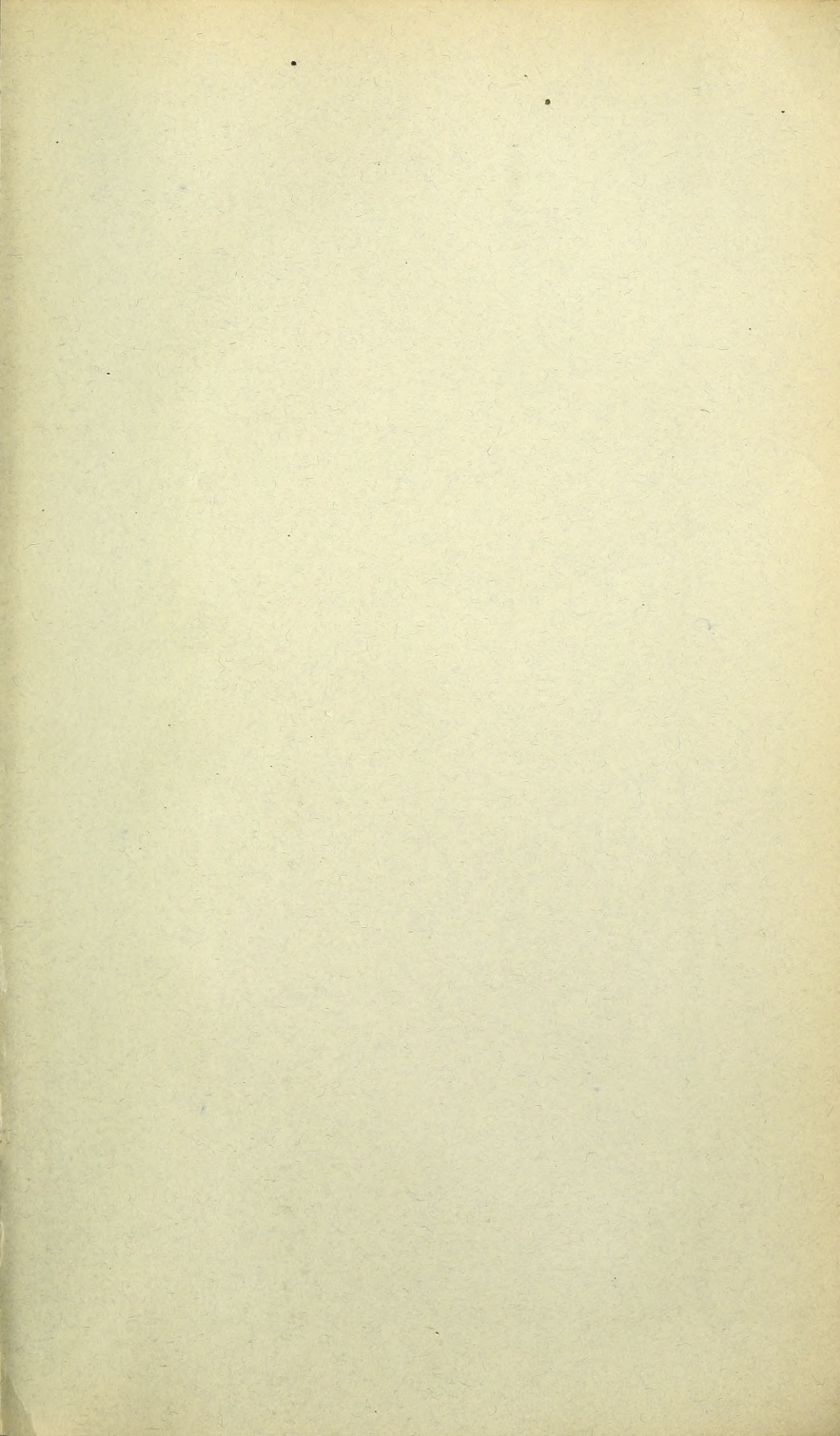
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